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Maximum Net Productivity Level Estimation for the Northern Fur Seal (*Callorhinus ursinus*) Population of St. Paul Island, Alaska

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Maximum Net Productivity Level Estimation
for the Northern Fur Seal (*Callorhinus ursinus*)
Population of St. Paul Island, Alaska

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ABSTRACT

Repetitive simulations are used to generate frequency distributions of maximum net productivity level estimates for the northern fur seal population of St. Paul Island, Alaska. Definitive determination of the maximum net productivity level is not possible due to uncertainty in life table parameters and density-dependent change in those parameters. This uncertainty is generally not accounted for in models used to study northern fur seal population dynamics. The repetitive simulation approach systematically varies simulation input parameters, runs a separate simulation with each input parameter combination, and validates the simulations on the basis of comparison with historical observations. Results from validated simulations form frequency distributions which provide a measure of confidence for estimates of the maximum net productivity level. These frequency distributions provide a basis for northern fur seal management that is more appropriate than single-point estimates, in that they reflect the current uncertainty regarding northern fur seal life history and density-dependent population regulation.

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INTRODUCTION

This study estimates the maximum net productivity level (MNPL) for the northern fur seal (*Callorhinus ursinus*) population of St. Paul Island, Alaska. The U.S. Marine Mammal Protection Act of 1972 (MMPA) established that marine mammal populations should not be allowed to diminish below their optimum sustainable population level. The U.S. National Marine Fisheries Service (Gehringer 1976) interpreted the lower limit for the optimum sustainable population level as the population's MNPL. Gehringer (1976) defined MNPL as the level at which there is "...the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality."

While the concept of MNPL is straightforward, its quantitative determination for natural marine mammal populations has proven to be difficult. Gerrodette and DeMaster (1990) reviewed methods for determining the status of a population relative to its MNPL by dividing them into those methods requiring estimation of the MNPL and those that do not. The methods reported here involve estimation of MNPL as an absolute abundance and as a fraction of the environmental carrying capacity (K). The simple (nongeneralized) logistic growth equation predicts that MNPL occurs when population abundance is $0.5K$, but there is both theoretical and empirical evidence that MNPL occurs at greater than $0.5K$ for large mammals (Gilpin et al. 1976, Eberhardt and Siniff 1977, and Fowler 1981). Fowler (1984,

1988) suggested that MNPL for Pribilof Island fur seal populations may be on the order of 0.6K, and as they are currently thought to be below this level, they have been designated as "depleted" under the MMPA. However, the precision of Fowler's (1984, 1988) estimate is not known, and there is uncertainty regarding the absolute abundance at which MNPL occurs and how to measure that abundance.

This paper considers three approaches to estimate MNPL. The first approach is based on analytical stock-recruitment models that were fit to fur seal data and then solved to provide estimates of MNPL. The second approach is based on numerical models of northern fur seal population dynamics that had been developed to simulate the recent history of the northern fur seal (Fig. 1). These simulations were reproduced and then examined for numerical estimates of MNPL. The first two approaches are described briefly to illustrate the nature of problems associated with their use to predict MNPL. The third approach is based on the numerical method of Smith and Polacheck (1984). This approach uses repetitive simulations to generate distributions of MNPL and MNPL/K estimates where the distributions are functions of the uncertainty in model input (i.e., input parameters and regulating mechanisms) and validation criteria (i.e., historical observations of the population used to validate model results). The distributions form a basis for judging the confidence that can be placed in any single estimate of MNPL.

ANALYTICAL APPROACH

Analytical stock-recruitment models have been used in the past to estimate the northern fur seal pup population size that results in the maximum return of juvenile males for the commercial harvest (Chapman 1961, 1964, 1973; Nagasaki 1961; Ichihara 1972; and Eberhardt 1981). There are three main difficulties associated with this approach for MNPL estimation.

The first difficulty results from the nature of northern fur seal data to which stock-recruitment functions can be fit. The data available are for number of pups born (stock) and number of animals surviving to age 2 or 3 (recruits); that is, these data represent only a segment of the population. But MNPL is a measure of the entire population determined under natural conditions without being confounded by age- or sex-selective harvests or other forms of human influence, either direct or indirect. Hence, the use of this stock-recruitment approach assumes that maximum net juvenile recruitment coincides with maximum net productivity of the whole population (Fig. 2). Do they coincide? Berkson and DeMaster (1985) have shown that the use of only a segment of a population can result in a biased assessment of whole-population trends, depending on the nature and timing of density-dependent regulation of the population. Thus, this stock-recruitment approach to estimating MNPL may include inherent bias.

The second difficulty associated with this analytical stock-recruitment approach is the reliability of the data. Initial

estimates of the number of pups born during the 1950s were based on animals tagged as pups and recovered as juveniles in the commercial harvest. However, these estimates were subsequently considered spurious (Chapman 1964, 1973), perhaps due to tag-induced mortality (but see also Smith and Polacheck 1984). The various published survival estimates for juvenile males (Fig. 3; Chapman 1973, Lander 1979, Smith and Polacheck 1984, and Trites 1989) are evidence that there remains substantial disagreement about the survival data. In addition, the uncertainty in number of pups born (the independent variable in these stock-recruitment functions) results in the errors-in-variables problem, which is not taken into account by standard regression techniques. As indicated by Walters and Ludwig (1981), "Errors in measuring ... stocks can have a profound effect on the appearance of stock-recruitment relationships."

A third difficulty involves the question of which stock-recruitment function to use. These stock-recruitment functions contain inherent mathematical bias. For example, it is well known that maximum net recruitment predicted by the familiar Beverton and Holt function (Beverton and Holt 1957) is mathematically constrained to less than $0.5K$. Hence, this function, and others with similar constraints, are too inflexible to accurately predict MNPL. Paulik (1973) suggested "asymptotic exponential regression" to make these models more flexible and thereby reduce their inherent bias. Other methods considered in this study involve the addition of a parameter to the models to

change the shape parameter to a linear or an exponential function of stock size. Chapman (1973) assessed this problem of model selection and concluded, "It would appear therefore that if we pick a particular stock-recruit model...to fit to real data, we are merely picking a convenient empirical curve which may have, but probably does not have, biological meaning." The selection of an appropriate model becomes critical if there is substantial variation in maximum net productivity levels predicted by the set of available stock-recruitment models.

To illustrate the problem of bias inherent in the models and the significance of model selection, twelve stock-recruitment functions were fit to female juvenile survival data (Fig. 4). Female juvenile survival was estimated using Chapman's (1973) data for male juvenile survival multiplied by his lambda factor of 1.1. Table 1 presents fitted parameter estimates, as well as resulting estimates of MNPL, K, and MNPL/K. The unmodified versions of the Robbins-Chapman (Robbins 1945, Chapman 1973), Ricker (1954), and Beverton and Holt (1957) models all predict MNPL/K to be less than 0.5. MNPL/K predictions from the modified versions of these models are all greater than 0.5, illustrating a reduction in bias resulting from the addition of a third parameter. However, the addition of a third parameter involves a trade-off; parameters for the modified versions of these models are estimated with less certainty, that is larger standard errors. Thus, while the addition of the third parameter appears to reduce bias in resulting MNPL estimates, it also results in greater variance about the parameter estimates

Table 1.--Fitted stock-recruitment curves, including modification of the Robbins-Chapman (Robbins 1945, Chapman 1973), Ricker (1954), and Beverton and Holt (1957) models. MNPL and K are given in thousands of pups born. The data fitted are adapted from Chapman (1973, p. 331, Table 112). Models followed by an asterisk (*) incorporate the additional parameter as suggested by Paulik (1973). Values under parameter estimates are coefficients of variation. R is recruits; S is stock; A, B, and C are parameters; "%" is (MNPL/K)*100; and Var is the variance about the regression or the sum of squared errors divided by the degrees of freedom. The designation "E" is base 10.

Model (R=)	A	B	C	MNPL	K	%	Var
<u>Robbins-Chapman</u>							
$A(1-e^{-BS})$	105.9 0.578	2.375E-3 0.933	-	206	452	46	317
$A(1-e^{-(B+CS)S})$	72.28 0.220	1.422E-3 2.743	1.180E-5 1.931	280	445	63	330
$A(1-e^{-BS e^{CS}})$	69.72 0.148	1.870E-3 1.030	3.576E-3 1.319	299	445	67	327
$A(1-e^{-BS^C}) *$	72.91 0.276	1.210E-4 5.760	1.649 0.685	277	445	62	330
<u>Ricker</u>							
ASe^{-BS}	0.2484 0.322	1.061E-3 0.772	-	211	450	47	316
$ASe^{-(B+CS)S}$	0.2265 1.047	4.529E-4 14.24	9.059E-7 10.44	234	448	52	333
$ASe^{-BS e^{CS}}$	0.2269 0.698	3.610E-4 7.648	2.063E-3 6.549	242	436	56	331
<u>Beverton and Holt</u>							
$\frac{1}{A+B/S}$	5.769E-3 0.780	3.856 0.444	-	198	456	43	318

Table 1.-- Continued.

Model (R=)	A	B	C	MNPL	K	%	Var
$\frac{1}{A+(Be^{CS}/S)}$	0.01329 0.297	8.662 1.680	-6.11E-3 1.491	277	445	62	331
$\frac{1}{A+B/S^C}^*$	0.01160 0.601	387.5 10.12	1.932 1.033	262	446	59	332
<u>Richards (as suggested by Eberhardt 1981)</u>							
$\frac{AS[(B/S)^{1-C}-1]}{1-C}$	10.68 0.089	466.8 0.014	60.01 0.799	422	452	93	286
<u>Generalized Allen (1972, from Chapman 1981)</u>							
$AS^B(K-S)^C$	6.127E-3 3.450	1.448 0.347	0.1741 0.593	365	464	79	286

and the resulting calculated MNPL. Confidence in the MNPL estimate is reduced. Figure 4 illustrates the fitted stock-recruitment curves. With the exception of the Richards curve (Richards 1959; bottom row, middle) and the generalized Allen (1972) curve from Chapman (1981; bottom row, right), the curves are remarkably similar in shape. It is important to note, however, that the predicted values of MNPL are markedly different, ranging from a population with 198,000 pups born to a population with 422,000 pups born. While the Richards curve and the generalized Allen curve give the best statistical fits (least variation about the regression), both of these curves indicate a very sharp decline in survival of females to age 3 as the

population approaches K. The sharpness of these declines is questionable and suggests an instability at large population abundance that is not consistent with the characterization of this species as being "K-selected."

Thus, it appears that this stock-recruitment approach is confounded by a number of sources of potential bias including 1) use of a segment of the population to index whole-population trends, 2) uncertainty in the data to which the stock-recruitment functions are fit, and 3) mathematical bias inherent in many of the functions. Reduction of the mathematical bias by the addition of a third parameter involves a trade-off with the degree of confidence in the resulting parameter estimates, and hence, the MNPL estimates calculated from the parameters. And finally, very similarly shaped stock-recruitment curves predict markedly different values of MNPL, but there is no apparent basis for choosing one stock-recruitment function over another.

These problems with the analytical approach clearly indicate that other methods of estimating MNPL are desirable. A second means of MNPL estimation for this northern fur seal population is with numerical models of fur seal population dynamics. This approach is considered in the following section.

NUMERICAL APPROACH

A variety of age-structured numerical models have been developed to simulate recent trends in northern fur seal abundance and to study the effects of various extrinsic

influences (e.g., harvests or fisheries interactions) on their populations. In the second stage of this work, models by Smith (1973), Eberhardt (1981, 1990), Swartzman (1984), and French and Reed (1989) were examined and reproduced to generate numerical estimates of MNPL. However, the results are not presented here because they reflect the same kinds of problems and uncertainty inherent in the stock-recruitment approach.

The original development of these numerical models involved choosing a life table of vital parameters and a mechanism of density-dependent regulation, then running a simulation and comparing it to historical observations (validation criteria), and finally, adjusting one or more elements of the model until the comparison was satisfactory, thus providing a basis for confidence in the model. The problems with this approach to MNPL estimation stem from uncertainty in the information required by the models. Uncertainty in model input (i.e., life table parameters and mechanism(s) of density dependence) suggests that there may be many apparently realistic combinations of parameters and density dependence which, when entered into a model, result in population simulations that are consistent with historical observations (i.e., satisfy the validation criteria). But the simulation patterns also indicate substantially different estimates of MNPL. The results from each of the above numerical models are based on a single combination of input information and therefore cannot reflect the uncertainty with which life table parameters and density dependence are known.

Uncertainty in life table parameters for the northern fur seal is indicated by the number of published survival and fecundity schedules (Kenyon et al. 1954, Chapman 1964, Eberhardt 1981, Goodman 1981, Lander 1981, Smith and Polacheck 1981, York and Hartley 1981, and Barlow and Boveng 1991). With the exception of Kenyon et al. (1954), survival and fecundity schedules have been developed primarily from data gathered in the extensive pelagic collection taken from 1958 to 1974 by Canadian and U.S. scientists. But these schedules differ with respect to assumptions of population equilibrium and methods of estimating survival of young females, which were underrepresented in the pelagic collection. Figure 5 illustrates the variability among four equilibrium survival schedules proposed for females.

Similarly, there is uncertainty about which of these parameters vary in response to changes in population abundance and the nature of that density-dependent change. The four models reproduced in this part of the study utilized different forms of density dependence, but applied that density dependence to juvenile survival only (Fig. 6); fecundity rates and survival rates of older animals were held constant. Yet, Smith and Polacheck (1981) argued that changes in juvenile survival alone could not account for the 8% change in population growth rate that occurred between 1912 and the 1950s. They point out that if two or more density-related mechanisms were responsible for the pattern of growth seen, then change in any one mechanism may have been small and therefore difficult to detect. Small changes in

adult female survival can have large regulatory effects (e.g., Eberhardt and Siniff 1977). But adult female survival is very difficult to measure, and previous estimates are imprecise relative to the degree of change necessary to substantially modify population growth. While there may not yet be clear evidence for density-related changes in fecundity and survival of fully mature adult females, the lack of evidence may reflect an inability to detect those changes when they occur. Density-dependent fecundity and adult survival should be considered as possible regulatory mechanisms in models of northern fur seal population dynamics.

The first two approaches (analytical models and numerical models with a selected parameter set) were described to illustrate the nature of the problems with the estimation of MNPL for northern fur seals. These approaches require data of uncertain accuracy and precision and utilize either stock-recruitment models or models of density dependence, both of which vary in their theoretical derivations and in their predictive properties. Consequently, it is difficult to judge the level of confidence that can be placed in the resulting estimates of MNPL.

REPETITIVE SIMULATIONS

To circumvent the above described problems, this study extended the modeling approach of Smith and Polacheck (1984). Their approach began by estimating the range of possible values for each of their model input parameters. The combination of all

the parameters constituted a "parameter space," that they systematically partitioned to form a large number of parameter combinations. Smith and Polacheck (1984) used their parameter combinations in separate simulations to study the effects of age structure and density dependence on the harvesting of northern fur seal females. In the present study, separate simulations using different parameter combinations were run to estimate possible values of MNPL. The results from the subset of simulations satisfying predetermined validation criteria created a distribution of MNPL estimates, providing a measure of confidence in individual estimates.

The Model

The model simulated the northern fur seals of St. Paul Island. The model population consisted of individuals of specified age and sex; males were included because MNPL applies to the entire population. Females were limited to a single pup each year, and the sex ratio of pups born was assumed to be 1:1. The model made discrete, yearly time steps from 1912 to 2000, with the annual cycle as depicted in Figure 7. The starting population was scaled to a stable age distribution producing 70,000 pups in 1912 (Kenyon et al. 1954). The commercial kill of juvenile males from 1918 to 1984 was not included in the model; males were subjected to natural sources of mortality only. The female kill from 1950 to 1968 was included, and females were removed by age according to records from the kill (Smith and

Polacheck 1984). The removal of females during any simulation occurred after MNPL was determined and was an important aspect of model validation. The pups of those females must have perished due to starvation; they were also removed from the model population (York and Hartley 1981).

Density Dependence

Life table values were divided into five parameter groups: adult (age 3 and older) female survival, fecundity (defined here as female births per female per year), juvenile (less than 3 years old) female survival, juvenile (less than 3 years old) male survival, and older (age 3 and above) male survival. In any simulation, adult female survival, fecundity, and juvenile female survival were varied independently in a density-dependent manner over some predetermined range or scope for density-dependent change. The nature of density-dependent change for adult female survival, juvenile female survival, and fecundity was determined by separate equations of the form (Allen 1976)

$$X_{i,t}(N_t) = X_i^* + (X_i' - X_i^*) (1 - (N_t/N^*)^Z), \quad (1)$$

where $X_{i,t}(N_t)$ = the value of parameter X for age i, year t, as a function of the number of females age 1 and older at the beginning of year t (N_t);

- X_i^* = the value of the parameter X_i at population equilibrium;
 X_i = the realized maximum value of parameter X_i ,
 N^* = the number of females age one and older at population equilibrium; and
 Z = a positive constant (shape parameter), specific to adult survival, fecundity, or juvenile survival.

The term $(X_i' - X_i^*)$ in Equation (1) is the difference between the "realized maximum value" for a parameter and its value when the population is at equilibrium; hence, it is the scope for density-dependent change in that parameter. For any given simulation, the realized maximum values of adult female survival (S_i') and fecundity (F_i') were determined by

$$S_i' = M_s (1.0 - S_i^*) + S_i^*, \text{ and} \quad (2)$$

$$F_i' = M_f (0.5 - F_i^*) + F_i^*, \quad (3)$$

where M_s and M_f are the proportion of the maximum possible scope for density-dependent change (Smith and Polacheck 1984; Fig. 8). Note that M_s and M_f apply simultaneously to all adult female survival values and all fecundity values, respectively. While it is biologically possible that juvenile survival could reach 1.0 yr⁻¹, it is clear that this value is never reached, and in this study "biologically possible" maximum values were arbitrarily

constrained for female pups to 0.8 yr^{-1} , for 1-year-old females to 0.9 yr^{-1} , and for 2-year-old females to 1.0 yr^{-1} . Hence, realized maximum survival values for female pups, 1-year-olds, and 2-year-olds were determined by

$$S_0' = M_j (0.8 - S_0^*) + S_0^*, \quad (4a)$$

$$S_1' = M_j (0.9 - S_1^*) + S_1^*, \text{ and} \quad (4b)$$

$$S_2' = M_j (1.0 - S_2^*) + S_2^*. \quad (4c)$$

M_j determined the realized maximum survival for all 3 age groups simultaneously in any given simulation. The use of 0.8, 0.9, and 1.0 yr^{-1} as biologically possible maximum values restricts female survival to age 3 and to no more than 0.72, which is consistent with the model of Smith (1973) and with the life table used by Goodman (1981) and Gerrodette et al. (1985).

The third term of the regulating function, $(1 - N_t/N^*)^Z$, determines the extent of parameter change between the realized maximum value and the equilibrium value as a function of the ratio of number of females age 1 and older at the beginning of year t (N_t) to the number of females age 1 and older when the population is at equilibrium (N^*). The value of Z , the shape parameter, controls the nonlinearity of the density-dependent regulating function (Equation 1). When Z is 1.0, the function is linear. As Z is increased above 1.0, the function becomes nonlinear and concave downward, and the nonlinearity increases as Z becomes larger (Fig. 9).

Survival for juvenile males was determined as a function of female juvenile survival. Chapman (1961, 1964, 1973) suggested survival of males and females from birth to age 3 can be related with the function

$$S_{0-3,m} = S_{0-3,f} / \lambda, \quad (5)$$

where $S_{0-3,m}$ and $S_{0-3,f}$ are survival from birth to age 3 for males and females, respectively, and λ is a constant equal to 1.1. Determined in this manner, survival of juveniles males was density-dependent in the same manner as survival of juvenile females. Survival of males older than age 3 was held constant in all simulations.

Parameter Values

Each simulation used a different combination of model input parameters. Parameter descriptions, ranges, and increments are listed in Table 2. Equilibrium life table values are listed in Table 3.

Validation Criteria

Five validation criteria were used to determine if the results of any given simulation were consistent with historical observations (Fig. 10). The first was the growth rate achieved during the interval 1912-24. Historical records suggest that the number of pups born annually during this period was growing

Table 2.--Input parameter descriptions, ranges, and increments as used in the repetitive simulations. Note that the parameter M_a was not allowed to exceed M_f in any simulation. These parameters determine the scope for density-dependent change as a portion of the maximum possible change in adult female survival and fecundity, respectively. Given this constraint, the partitioning of input parameters as listed results in 8,468,064 possible parameter combinations, each of which was tested in a separate simulation.

Parameter	Description	Range	Increment
P_{eq}	Total number of pups born with the population at equilibrium and in stable age distribution	350-500,000	10,000
M_a	Determines realized maximum adult female survival as a portion of maximum possible scope for change	0.0 - 1.0	0.1
M_f	Determines realized maximum fecundity as a portion of maximum possible scope for change	0.0 - 1.0	0.1
M_j	Determines realized juvenile survival as a portion of maximum possible scope for change	0.0 - 1.0	0.1
Z_a	Exponent determining nonlinearity of Allen function regulating adult female survival	1.0 - 5.0	0.5
Z_f	Exponent determining nonlinearity of Allen function regulating fecundity	1.0 - 5.0	0.5
Z_j	Exponent determining nonlinearity of Allen function regulating juvenile survival	1.0 - 5.0	0.5

at the rate of about 0.08 yr^{-1} (Kenyon et al. 1954). Pups were enumerated in those years, and while the counts are generally accepted, the possible error may be substantial. Gerrodette et al. (1985) simulated the growth of a northern fur seal population

Table 3.--Equilibrium life table values used in the simulations.
 Female survival rates taken from Barlow and Boveng
 (1991), pregnancy rates modified from Smith and Polacheck
 (1984), and male survival rates modified from Lander
 (1981).

Age	Females			Males	
	Annual Survival Rate p_x	Survival from Age 0 l_x	Annual Birth Rate m_x	Annual Survival Rate p_x	Survival from Age 0 l_x
0	0.539	1.000	0.000	0.522	1.000
1	0.702	0.539	0.000	0.680	0.522
2	0.814	0.378	0.000	0.789	0.355
3	0.885	0.308	0.010	0.800	0.280
4	0.928	0.273	0.015	0.800	0.224
5	0.951	0.253	0.220	0.800	0.179
6	0.964	0.241	0.395	0.800	0.143
7	0.969	0.232	0.395	0.800	0.115
8	0.969	0.225	0.425	0.800	0.092
9	0.964	0.218	0.460	0.760	0.073
10	0.956	0.210	0.445	0.730	0.056
11	0.943	0.201	0.450	0.700	0.041
12	0.923	0.189	0.440	0.650	0.029
13	0.894	0.175	0.430	0.590	0.019
14	0.854	0.156	0.420	0.540	0.011
15	0.799	0.133	0.410	0.430	0.006
16	0.726	0.107	0.390	0.000	0.003
17	0.631	0.077	0.350	0.000	0.000
18	0.515	0.049	0.305	0.000	0.000
19	0.384	0.025	0.264	0.000	0.000
20	0.000	0.000	0.025	0.000	0.000

under conditions similar to those in the 1910s and determined the 99% confidence interval for the growth rate to fall between 0.048 yr^{-1} and 0.115 yr^{-1} . In this study, growth rate values of 0.05 yr^{-1} and 0.11 yr^{-1} (which corresponds to a counting error of approximately 15%) were used as lower and upper limits to the annual growth rate between 1912 and 1924. Simulations with annual growth rates outside this range were not continued.

The second criterion was the number of pups born annually in the interval 1940-55. Smith and Polacheck (1984) estimated the lower limit of pup population size during that period as 350,000. If the maximum pup number in the model during this period did not reach 350,000, the simulation was discontinued.

The third criterion was based on the generally accepted idea that the population was near equilibrium by the late 1940s or early 1950s. If growth rate for the population did not decline to less than 0.015 yr^{-1} (arbitrarily chosen) during the interval 1945-55, the simulation was stopped.

The fourth criterion was the number of pups born annually in the interval 1962-70. The shear-sample (mark-recapture) technique for estimating pup numbers (Chapman and Johnson 1968) was used during this period and the counts are considered relatively reliable. These pup estimates have been used to validate models in earlier studies (Smith 1973, Eberhardt 1981 and 1990, Smith and Polacheck 1984, French and Reed 1989, and Trites and Larkin 1989). The maximum number of pups estimated for this period was about 298,000 (Briggs and Fowler 1984, Smith

and Polacheck 1984). Allowing for 15% error in this estimate, the fourth criterion stopped the simulation if the minimum count during this period 1962-70 was greater than 342,700.

The fifth criterion was the presence/absence of growing oscillations in total population abundance or other abnormal behavior. If a simulation passed the other criteria, it was allowed to run until the year 2000. The simulation was considered unacceptable if 1) prior to the female harvest 1956-68 the total population growth rate became negative and the magnitude of the decline was greater than 0.1 yr^{-1} ; 2) between 1970 and 2000 the total population growth rate was positive with a magnitude greater than 0.2 yr^{-1} or negative with a magnitude greater than 0.1 yr^{-1} ; 3) there were at least three oscillatory cycles between 1970 and 2000, and the difference between the third peak and third trough was greater than the difference between the second peak and second trough; or 4) between 1970 and 2000 the total population dropped to less than the minimum population size recorded during the female harvest.

Measurements and Sensitivity

Five population measures, including MNPL, K, the number of pups born at MNPL and K, and the ratio MNPL/K were recorded for each simulation that passed the validation criteria. MNPL was determined numerically by locating the total population size resulting in the maximum net annual increment in population growth; the number of pups born at that population size was also

recorded. The number of pups born at equilibrium was a simulation parameter that was used with the equilibrium life table to calculate the population size at K; K was not determined numerically. The abundance of pups was recorded for each successful simulation to compare with observed pup estimates, which are the most reliable measures of the natural population.

To select those simulations that were most consistent with historical records, an error was calculated for each successful simulation. The error was based on observed and modeled pup numbers from 1962 to 1970. Assuming that the standard error in pup estimates from this period was proportional to the size of the pup population, the error was calculated as

$$\text{error} = \sum_{t=1962}^{1970} [\ln(N_{0,t,m}) - \ln(N_{0,t,o})]^2, \quad (6)$$

where \ln is the natural logarithm, $N_{0,t,m}$ is the year-specific pup production in the model, and $N_{0,t,o}$ is the observed annual pup production reported in Briggs and Fowler (1984). Error calculations do not extend beyond 1970 as there is evidence that population trends, including pup production, were substantially confounded after 1970 by injuries and death due to entanglement in marine debris (Fowler 1985). Frequency distributions were reconstructed using successful simulations weighted inversely by their error. Additional distributions were constructed using only those simulations with an error in the lower 10% of the

error range. Finally, to test the sensitivity of the distributions resulting from this approach, the simulations were subjected to modified validation criteria and to modifications of various model assumptions.

RESULTS

Simulations With Original Validation Criteria

Of the 8,468,064 simulations attempted, 736,629 (8.7%) passed the original validation criteria. Estimates of MNPL, pups born at MNPL, K, pups born at K, and the ratio MNPL/K from these successful simulations were used to construct the frequency distributions shown in Figure 11. Maximum net productivity level in these simulations ranged from a total abundance of about 0.8 million to 1.2 million, with a mode at 0.98 million (Fig. 11A). Corresponding estimates of pups born at MNPL (Fig. 11B) ranged from about 185,000 to just over 300,000 with a mode at 243,000 pups born. Estimates of the ratio MNPL/K (Fig. 11C) ranged approximately from 0.5 to less than 0.8 with a mode at 0.65. Estimates of the total population size at K ranged from 1.43 million to about 1.8 million with a mode at 1.47 million, corresponding to the production of 350,000 to 440,000 pups with a mode at 360,000. Estimates of MNPL, pups born at MNPL, and MNPL/K appeared to be normally distributed. Left truncation of the distribution for estimates of K and pups born at K (Fig. 11D) resulted from the use of pups born at K as an input parameter for the model with an imposed lower limit of 350,000 pups. Recall

that estimates of total population size at K were calculated from the number of pups born at K and the equilibrium life table, hence, the identical distributions.

Simulations With Modified Validation Criteria

Narrowing the acceptable range for the annual growth rate between 1912 and 1924 from 0.05-0.11 to 0.06-0.10 resulted in fewer simulations being accepted (6.2%; $n = 524,362$). Reductions in the distributions appeared to be proportional (Fig. 12), with ranges and modes essentially unchanged. The largest change was a shift in the modal value for pups born at MNPL from 243,000 to 237,000 (Fig. 12B).

Decreasing the upper limit for minimum growth rate during the period 1940 to 1955 from 0.015 yr^{-1} to 0.01 yr^{-1} had a negligible effect on the original distributions of population measures (8.6% accepted; $n = 731,633$; results not shown).

Increasing the lower limit for the maximum number of pups born annually between 1945 and 1955 from 350,000 to 381,000 resulted in a substantial reduction in the number of successful simulations (4.1%; $n = 347,208$). In addition, there was a shift of the MNPL distribution and the combined distribution for K and pups born at K to larger values (Fig. 13). Distributions of pups born at MNPL and MNPL/K were less affected by modification of this validation criterion in that the mode changed very little.

Additional Results

A test of the sensitivity of this modeling approach to the method of partitioning the parameter space was conducted by changing the increment size for M_1 and M_2 from 0.1 to 0.2. That is, these parameters were allowed to assume only six values (0.0, 0.2, 0.4...1.0) instead of eleven (0.0, 0.1, 0.2...1.0). With this adjusted partitioning, 2.6% of the simulations were successful ($n = 220,034$). The disproportionate decline in number of cases meeting validation criteria is discussed below. However, locations of the distributions appeared to be essentially unchanged (Fig. 14).

Weighting of population measures by the inverse of the error in pup estimates during the interval 1962-70 resulted in only slight shifts in the distributions (Fig. 15). The largest modal shift was in the number of pups born at MNPL, which declined to 234,000 from 243,000. However, when only those simulations with errors in the lowest 10% of the error range were considered ($n = 6,279$), there were large downward shifts in all distributions, particularly the number of pups born at MNPL (Fig. 16).

Included in Figure 17 are the age-specific equilibrium survival rates for females from Barlow and Boveng (1991). When these equilibrium survival values were adjusted to be more consistent with other published equilibrium survival schedules (Figs. 5 and 17), substantial changes occurred in number of successful simulations (20.0%; $n = 1,697,491$) and distributions

of the population measures (Fig. 18). The modal MNPL estimate increased to 1.04 million and there was a clear shift in this distribution to higher values. Number of pups born at MNPL also increased to higher values with a mode at 261,000 pups born. The distribution of MNPL/K shifted to slightly lower values, but the mode was essentially unchanged at 0.64. The combined distribution for K and the number of pups born at K shifted upward with the mode for the total population at approximately 1.6 million, producing from 360,000 to 370,000 pups.

Reduction of biologically possible maximum values for adult survival and fecundity from 1.0 yr^{-1} and 0.5 yr^{-1} to 0.98 yr^{-1} and 0.49 yr^{-1} , respectively, resulted in fewer successful simulations (5.9%; $n = 499,887$; results not shown), but distribution locations were essentially unchanged. However, when maximum change possible in adult survival or fecundity was limited to no more than 10% of equilibrium value (Fig. 17), then 12.1% of the attempted simulations were successful ($n = 1,026,284$; Fig. 19). Under this constraint, distributions of MNPL and MNPL/K shifted to larger values, with modal values of 1.04 million animals and 66%, respectively. The distribution of pups born at MNPL shifted to lower values, with a modal value of 237,000 pups. Population size at K and number of pups born at K were much more evenly distributed throughout the approximate range of 1.43-1.71 million animals with 350,000 to 420,000 pups born. While the modal value did not change, there was a clear shift toward larger values.

For each successful simulation corresponding to the original validation criteria (Fig. 10), values of M_i , M_r , and M_j were recorded. Distributions of M_r and M_j were strongly skewed to higher values, while the distribution of M_i values was strongly skewed to lower values (Fig. 20). Recall from Table 2, however, that the value of M_i in any given simulation was never allowed to exceed M_r ; hence, relatively fewer simulations were run with larger values of M_i .

Values of Z_i , Z_r , and Z_j were also recorded for each successful simulation, and the effect of nonlinearity on the ratio $MNPL/K$ is presented in Figure 21 for several values of M_i , M_r , and M_j .

DISCUSSION

This repetitive simulation approach is designed to account for the fundamental problem of uncertainty in northern fur seal life history parameters and mechanisms of density-dependent regulation. Clearly, a consequence of this uncertainty is that satisfaction of the validation criteria is a basis for only limited confidence in any given simulation. Repetitive simulations illustrate that many combinations of parameters and regulating mechanisms lead to satisfaction of the validation criteria, even though these combinations represent only a small portion of the parameter space. Frequency distributions of results from the complete set of successful simulations provide a

basis for more confidently identifying critical reference population levels.

The main components of this approach include: 1) validation criteria, 2) equilibrium life table parameters and scope for density-dependent change in those parameters, 3) functions representing population regulation, and 4) a method of partitioning the parameter space to create parameter combinations for testing in separate simulations. Each of these components is discussed below.

Validation Criteria

Results from this repetitive simulation approach appear to be robust to changes in the allowable annual growth rates in the intervals 1912-24 and 1945-55. Results were more sensitive to the validation criterion based on number of pups born annually in the interval 1940-55. As mentioned earlier, there is a great deal of uncertainty about true pup production during this period. York (1985) suggested the number of pups born in 1940 on St. Paul Island may have been as high as 469,315. Fortunately, the frequency distributions for the number of pups born at MNPL and the ratio MNPL/K appear to be less sensitive to this criterion than are the distributions for population size at MNPL and K.

The fourth validation criterion was the number of pups born annually during the interval 1962-70. Because estimates of pup production during this period are considered relatively reliable, they were not used to test the sensitivity of the distributions

of the five population measures. Rather, as described earlier, they were used to weight successful simulations on the basis of the error between simulated and observed numbers. The weighting of successful simulations did not alter the distributions substantially, unless only simulations with an error in the lowest 10% of the error range were considered. These "best" simulations were most consistent with historical observations, and suggest that all five population measures are overestimated by the original results (Fig. 16). As pup production is the best index of this population, the discrepancy in predictions of number of pups born at MNPL is particularly disturbing.

The fifth validation criterion was intended to reject simulations exhibiting behavior assumed to be unrealistic for this population. One of the most difficult aspects of this approach involved the detection and rejection of "unnatural" oscillations in population abundance. For example, trial simulations using the number of pups as the measure of density resulted in 2.2% of the simulations passing the validation criteria, far fewer than when the number of females age 1 and older was used. Presumably, the difference was due to unnatural oscillations from fluctuating pup numbers and the effects of that fluctuation on fecundity and adult survival rates as calculated annually in the model. When millions of simulations are run, the behavior of all individual simulations can not be visually monitored. While it was not done in this study, a random sample

of rejected simulations may be useful in characterizing unnatural behavior in the simulated population.

Life Table Parameters and Scope for Density-Dependent Change

As illustrated in Figure 5, there is substantial uncertainty in equilibrium life table parameters for the northern fur seal. This life table determines the age structure of the population at equilibrium, and as used here, also determines the scope for density-dependent change in parameters. The equilibrium survival schedule of Barlow and Boveng (1991) was used in this study because it includes survival rate estimates for all ages, and because it changes with age in a smooth rather than abrupt, manner. Their survival schedule combines relatively low juvenile survival with high adult survival, allowing greater scope for density-dependent change at younger ages. As indicated in Figure 18, the use of a different life table resulted in a substantial difference in the number of successful simulations, as well as in estimates of total and pup population sizes at MNPL and K. Figure 20 indicates that density-dependent change in adult survival is likely to be small, whereas similar change in fecundity and juvenile survival is likely to be large. As Smith and Polacheck (1981) pointed out, we are unable to detect small changes in adult survival that may have significant influence on population regulation. The need to refine estimates of northern fur seal life table values is emphasized both by the sensitivity of results obtained here and by the present inability to detect

changes in life table values that may have significant regulatory effects. This has proven to be difficult due to the lack of information on younger age classes and the required assumption of population equilibrium.

Regulatory Function

A single functional form (Allen 1976) was used in this study to regulate adult female survival, fecundity, and juvenile survival. Varying the scope for density-dependent change and the exponent (Z) controlling the degree of nonlinearity allows this functional form to exhibit a wide range of possible behaviors (Fig. 9). Its relative continuity over the tested values of Z was a useful property for compiling frequency distributions. Still, this form, as used here, may have been too restrictive and additional functions should be tested. For example, density-dependent parameter change corresponding to a Z -value of 5 is not as nonlinear as the function of Eberhardt (1981) for female juvenile survival. An altogether different function might not easily be modified to generate frequency distributions, but perhaps could be compared with results for a particular value of Z .

The effects of nonlinearity in this function on the ratio $MNPL/K$ are seen in Figure 21. As the exponent Z becomes larger, there is a general increase in the ratio $MNPL/K$. However, these increases are not large, and it appears that this ratio is strongly conserved or robust in this modeling approach. In

general, the effect of nonlinearity should increase as the scope for density-dependent change becomes larger. This appears to be the case, although the differences are not large and are difficult to evaluate when there are few successful simulations (e.g., adult survival with large scope for density-dependent change). With respect to fecundity, there appears to be a trade off between the degree of nonlinearity and the number of successful simulations. That is, when Z_f is large, there are fewer acceptable simulations. But this does not appear to be the case for adult or juvenile survival. It is surprising that MNPL/K appears to be least affected by changing nonlinearity in adult survival, again suggesting that this ratio is highly conserved.

In addition to the exponent Z , another important element of this functional form is the variable used as the measure of density. The true mechanism(s) of density-dependent change in northern fur seal life table parameters has not been determined. Hence, it is difficult to know what portion of the population best serves as an index of population density. For example, if food is the limiting factor, then it is important to know how food availability limits population growth and what age and sex groups are competing for the same limiting food resource. Again, this information is not currently available. In this study, the number of females age 1 and older was used as the measure of density, but it is reasonable to suspect that these results might be altered with some other measure.

Partitioning of the Parameter Space

The presentation of results in Figures 11-14, 18, and 19 assumed that each simulation outcome was equally likely. This implies that the probability distributions for the parameters in the life table and regulating mechanisms were also equally likely, which seems unrealistic. However, because probability distributions were not known for the model parameters, and the nature of regulation was uncertain, the assumption of uniform or equal probability for all simulations was used as a first approximation.

It was also assumed that true parameter values and regulating mechanisms were encompassed in the ranges tested, and that the method of partitioning the parameter space did not distort the resulting frequency distributions. The possibility that the method of partitioning may bias the resulting frequency distributions should be more fully investigated. An initial test of the effect of partitioning was conducted by reducing the number of values that M_1 and M_2 could assume (Fig. 14). If the values tested for these parameters were equally likely, then the corresponding reduction in the number of successful simulations was expected to be 45%. The observed reduction was 70%. This was consistent with the results in Figures 20 and 21, which also suggested the tested values of M_1 and M_2 were not equally likely.

The partitioning of the parameter space is important for another reason. A large number of input parameters can lead to a

large number of parameter combinations (8,468,064 in this study); running a separate simulation with each parameter combination consumes extensive computing resources.

Concluding Remarks

This investigation of MNPL attempted to account for the uncertainty in life history parameters and density-dependent regulation of the northern fur seal population of St. Paul Island, Alaska. While single stock-recruitment forms and single numerical simulations can provide single estimates of MNPL, they provide little indication of the confidence that can be placed in those estimates and fail to account for the fundamental uncertainty of the required data and assumptions. MNPL for marine mammal populations will never be known with complete certainty. The issue is not simply how to find a best estimate, but also how to assess the probability and implications of alternative estimates.

The strategy used in this study is, in effect, an extension of sensitivity testing. Model sensitivity is frequently evaluated simply by adjusting single parameters (dimensions) around their mean values to explore a parameter space in the neighborhood of a most likely solution. The systematic approach used here explores the entire parameter space, and thereby also considers the interaction of the different parameters.

This approach requires extensive data and computing resources. Data are always insufficient, which emphasizes the

need to deal with uncertainty. But to the extent that they are available, such data provide a means for generating frequency distributions of theoretical population levels. With less data the dispersion will be greater -- an important consideration in population management. In the case of the northern fur seal, for which there is more data than most species, these distributions clearly demonstrate that MNPL, K, pups born at MNPL and K, and MNPL/K may occur over a wide range of population levels, and that definitive estimates cannot be obtained without making unwarranted assumptions regarding life table values and density-dependent mechanisms.

Finally, it is suggested that these frequency distributions can serve as first approximations of probability distributions for these theoretical reference levels. As such, these distributions suggest that it is highly likely that the current population level (producing on the order of 200,000 pups) is well below MNPL.

However, the question of how these distributions are used is not entirely a scientific issue. Here, description of these distributions has been limited to modes and ranges. For management purposes, some other descriptor may be more important. Based on the current statistical paradigm, the 95th percentile may be considered a more conservative, useful value from these distributions. In any case, these distributions reflect the uncertainty with which the natural history of the northern fur

seal is known, and they thereby provide a more realistic scientific and management perspective.

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LIST OF FIGURES

Fig. 1. Number of northern fur seal pups born annually on St. Paul Island, Alaska, from 1912 to 1990. Simulations (described later in the text) were conducted to reproduce this time series, filling in the large gap between 1925 and the late 1940s. Data are from Briggs and Fowler (1984).

Fig. 2. A. Hypothetical maximum net recruitment of 3-year-old northern fur seal females as a function of the number of pups born. The vertical distance between the replacement and recruitment lines corresponds to net recruitment. Maximum net recruitment occurs where the slope of the recruitment line equals the slope of the replacement line and is defined here in terms of a specific portion of the population. B. MNPL as predicted by the simple (nongeneralized) logistic model and as may occur (hypothetically) for the northern fur seal. MNPL is defined here in terms of the whole population. Maximum net recruitment of 3-year-old females and maximum net productivity of the whole population do not necessarily occur at the same population level; hence, the population producing the maximum net recruitment of 3-year-old females may be a biased indicator of MNPL.

Fig. 3. Estimates of male survival from birth to age 3 in Chapman (1973) and Smith and Polacheck (1984), and from birth to age 2 in Lander (1979) and Trites (1989). Note differences in ages for which survival is evaluated and in the years for which data are included.

Fig. 4. Stock-recruitment models from Table 1 used to fit estimated recruitment of 3-year-old females (Y-axes) to number of pups born (X-axes). Data are adapted from Chapman (1973) and are for the years 1920-22 and 1950-65. Except for the generalized logistic (Richards 1959 and Allen 1976) models (middle and right of bottom row, respectively) the fitted models are visually similar. However, these models result in substantially different estimates of MNPL (left triangles just above X-axes). Estimates of K (right triangles) are much less variable.

Fig. 5. Variability in age-specific equilibrium survival rates for female northern fur seals from the life tables of Lander (1981), York and Hartley (1981), Smith and Polacheck (1981), and Barlow and Boveng (1991).

Fig. 6. Density-dependent mechanisms used in numerical modeling of northern fur seal population dynamics, including female survival from birth to age 3 (Smith 1973 and Eberhardt 1981), on-land pup survival (Swartzman 1984), and survival for the first 20 months at sea as a function of on-land survival (Lander 1979).

Fig. 7. The annual cycle of northern fur seals as modeled in these repetitive simulations.

Fig. 8. Realized maximum values and scope for density-dependent change of life table parameters as determined by the input parameters M_1 , M_4 , and M_5 (from Smith and Polacheck 1984). See Table 2 for biologically possible maximum values and equilibrium values.

Fig. 9. Density dependence of vital parameters determined by the general Allen (1976) function and used by Smith and Polacheck (1984). Each line is labeled with the Z value used to generate that line.

Fig. 10. The five validation criteria used to accept or reject simulations. The first criterion was the growth rate in the interval 1912-24. If the growth rate was within acceptable limits, the pups numbers passed between the two arrows on the left. The second criterion was the lower limit (350,000) for the maximum annual pup number in the interval 1940-55. The third criterion was the annual growth rate in the interval 1945-55, which had to decrease to less than 0.015 for at least 1 year. The fourth criterion was the number of pups born annually in the interval 1962-70, which must have dropped to less than 342,700 for at least 1 year. The final criterion rejected the simulation on the basis of abnormal behavior, particularly growing oscillations after 1970. Hollow circles are the pup numbers from a simulation. Also shown (filled circles) are the pup estimates for the interval 1962-70 from Briggs and Fowler (1984).

Fig. 11. Frequency distributions for five population measures from simulations satisfying original validation criteria ($n = 736,629$). Population measures include A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K.

Fig. 12. Frequency distributions for five population measures ($n = 524,362$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Growth rates limits for interval 1912-24 narrowed to 0.06 and 0.10. The dotted line corresponds to results from Figure 11, with the original validation criteria (where growth rate limits were 0.05 to 0.11).

Fig. 13. Frequency distributions for five population measures ($n = 347,208$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Lower limit for maximum annual number of pups born in the interval 1940-55 increased from the initial level of 350,000 to 381,000. The dotted line corresponds to results from Figure 11, with the original validation criteria.

Fig. 14. Frequency distributions for five population measures ($n = 220,034$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. M_1 and M_2 parameters limited to six values (0.0, 0.2, 0.4...1.0) rather than eleven (0.0, 0.1, 0.2...1.0). The dotted line corresponds to results from Figure 11.

Fig. 15. Relative frequency distributions for five population measures ($n = 736,629$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Distributions are weighted by the error between observed annual pup production and pups born in the model during the interval 1962-70. The dotted line corresponds to results from Figure 11. To facilitate comparison, all distributions are scaled to sum 1.0.

Fig. 16. Relative frequency distributions for five population measures ($n = 6279$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Distributions are weighted by the error between observed annual pup production and pups born in the model during the interval 1962-70. Only simulations with error in the lower 10% of the error range are included. The dotted line corresponds to results from Figure 11, with the original validation criteria. To facilitate comparison, all distributions are scaled to sum 1.0.

Fig. 17. Comparison of age-specific survival values for northern fur seal females as used in the repetitive simulations, including equilibrium values from Barlow and Boveng (1991), adjusted equilibrium values with slightly greater juvenile survival and lower adult survival (modified arbitrarily but constrained to result in equilibrium growth), and an adjusted schedule of biologically possible maximum values (biologically possible values limited to no more than 10% of corresponding equilibrium values). The latter two survival schedules were used to test the sensitivity of the repetitive simulation approach to a different life table and to limited scope for density-dependent change, respectively.

Fig. 18. Frequency distributions for five population measures ($n = 1,697,491$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Results generated using an adjusted equilibrium survival schedule for females (see Fig. 17). The dotted line corresponds to results from Figure 11, with the equilibrium survival schedule from Barlow and Boveng (1991).

Fig. 19. Frequency distributions for five population measures ($n = 1,026,284$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Results generated by limiting the scope for density-dependent change in adult survival to no greater than 10% of the equilibrium value (see Fig. 17). The dotted line corresponds to results from Figure 11, where a biologically possible maximum value of 1.0 was used for all adult female survival rates.

Fig. 20. Frequency distributions for values of M_s , M_f , and M_j recorded from successful simulations ($n = 736,629$).

Fig. 21. Frequency distributions of MNPL/K as determined by degree of nonlinearity (Z_s , Z_f , or Z_j) and scope for density-dependent change (M_s , M_f , or M_j) in the functions regulating adult female survival, fecundity, and juvenile survival, respectively.

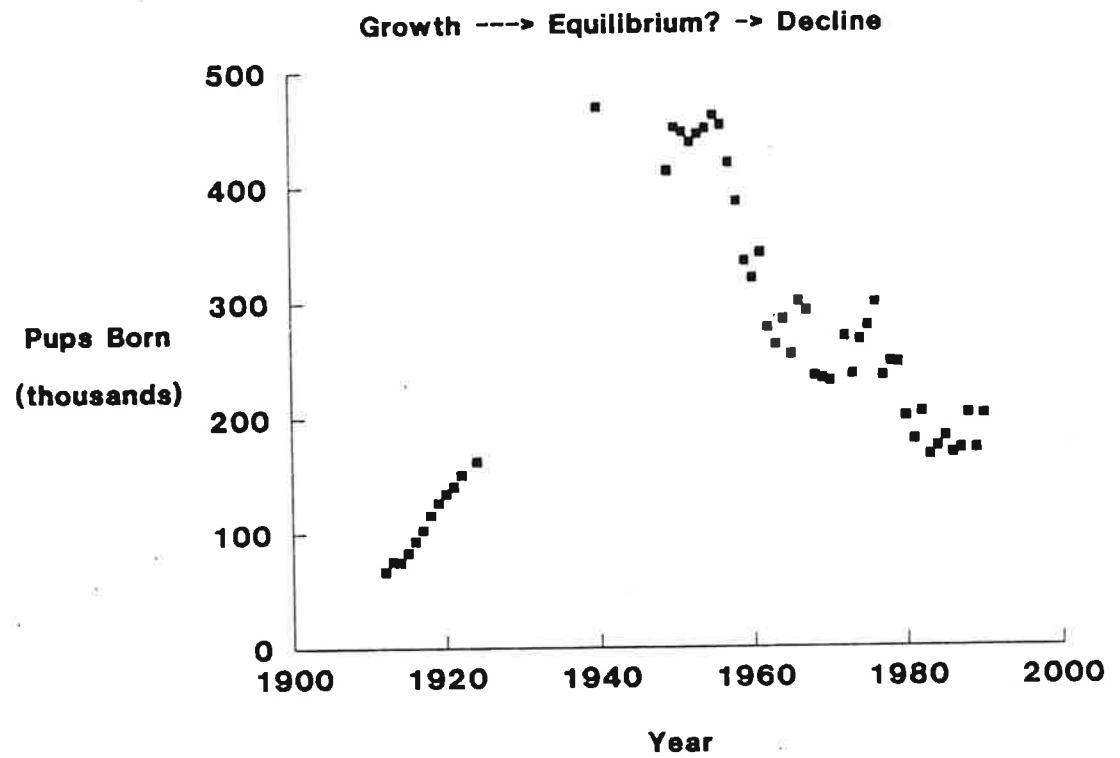


Fig. 1. Number of northern fur seal pups born annually on St. Paul Island, Alaska, from 1912 to 1990. Simulations (described later in the text) were conducted to reproduce this time series, filling in the large gap between 1925 and the late 1940s. Data are from Briggs and Fowler (1984).

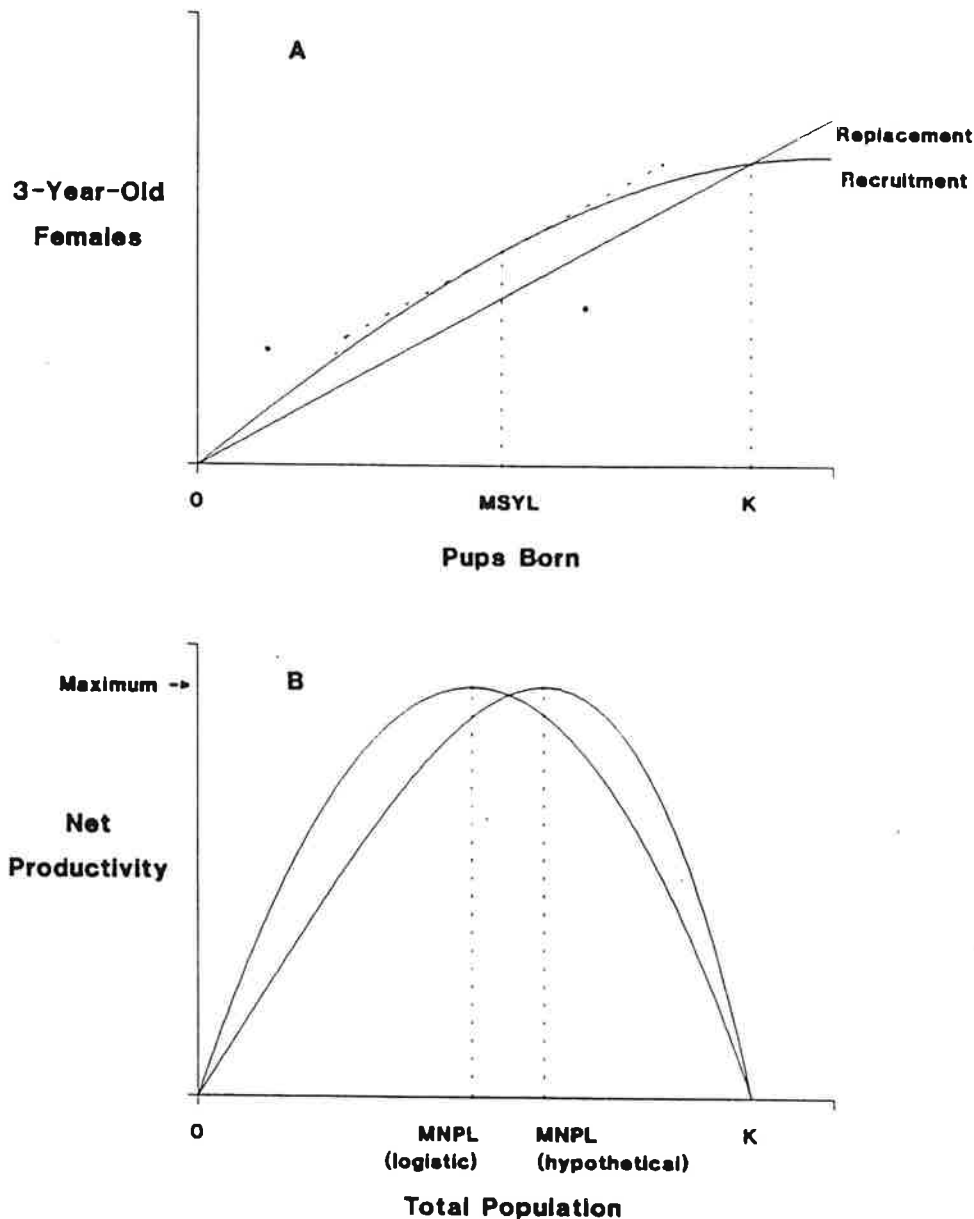


Fig. 2. A. Hypothetical maximum net recruitment of 3-year-old northern fur seal females as a function of the number of pups born. The vertical distance between the replacement and recruitment lines corresponds to net recruitment. Maximum net recruitment occurs where the slope of the recruitment line equals the slope of the replacement line and is defined here in terms of a specific portion of the population. B. MNPL as predicted by the simple (nongeneralized) logistic model and as may occur (hypothetically) for the northern fur seal. MNPL is defined here in terms of the whole population. Maximum net recruitment of 3-year-old females and maximum net productivity of the whole population do not necessarily occur at the same population level; hence, the population producing the maximum net recruitment of 3-year-old females may be a biased indicator of MNPL.

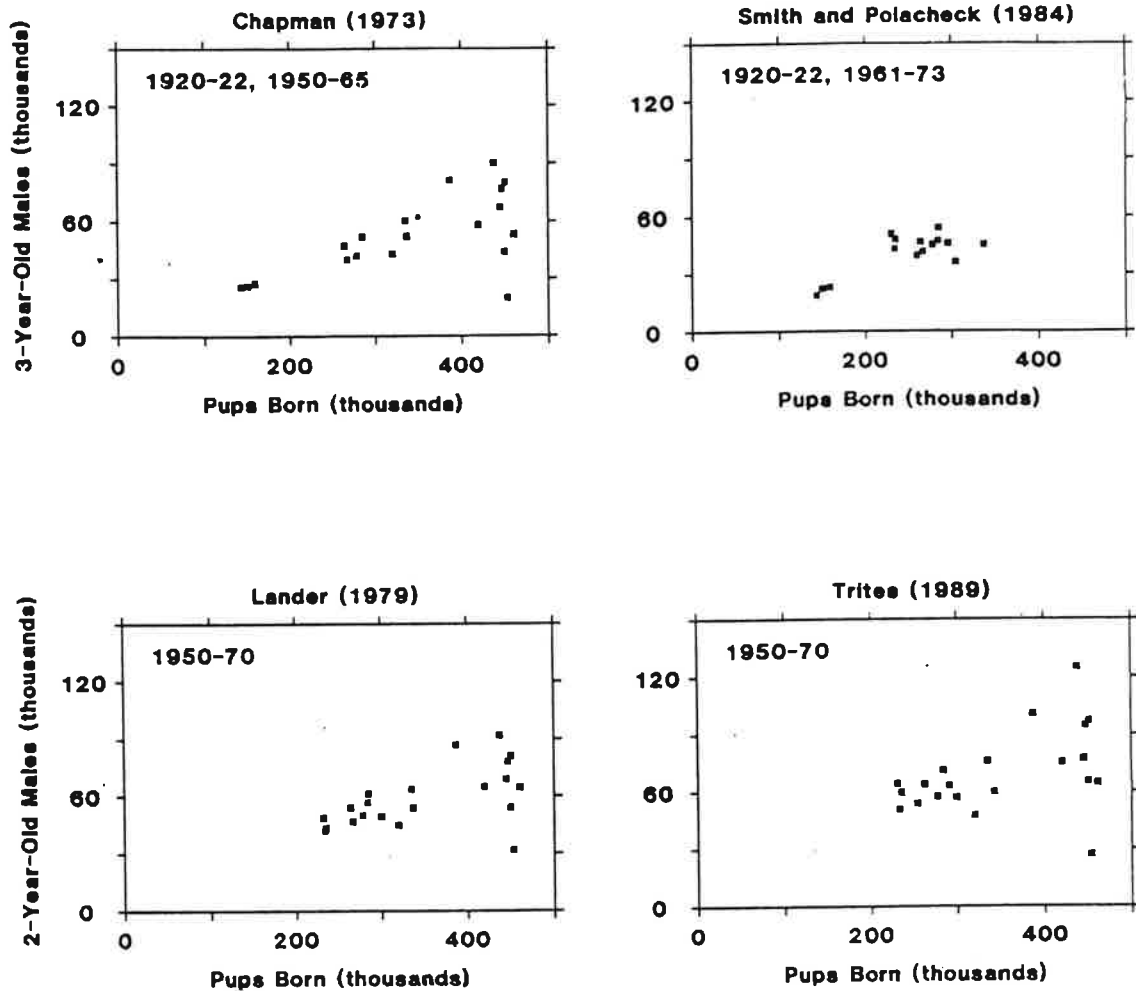


Fig. 3. Estimates of male survival from birth to age 3 in Chapman (1973) and Smith and Polacheck (1984), and from birth to age 2 in Lander (1979) and Trites (1989). Note differences in ages for which survival is evaluated and in the years for which data are included.

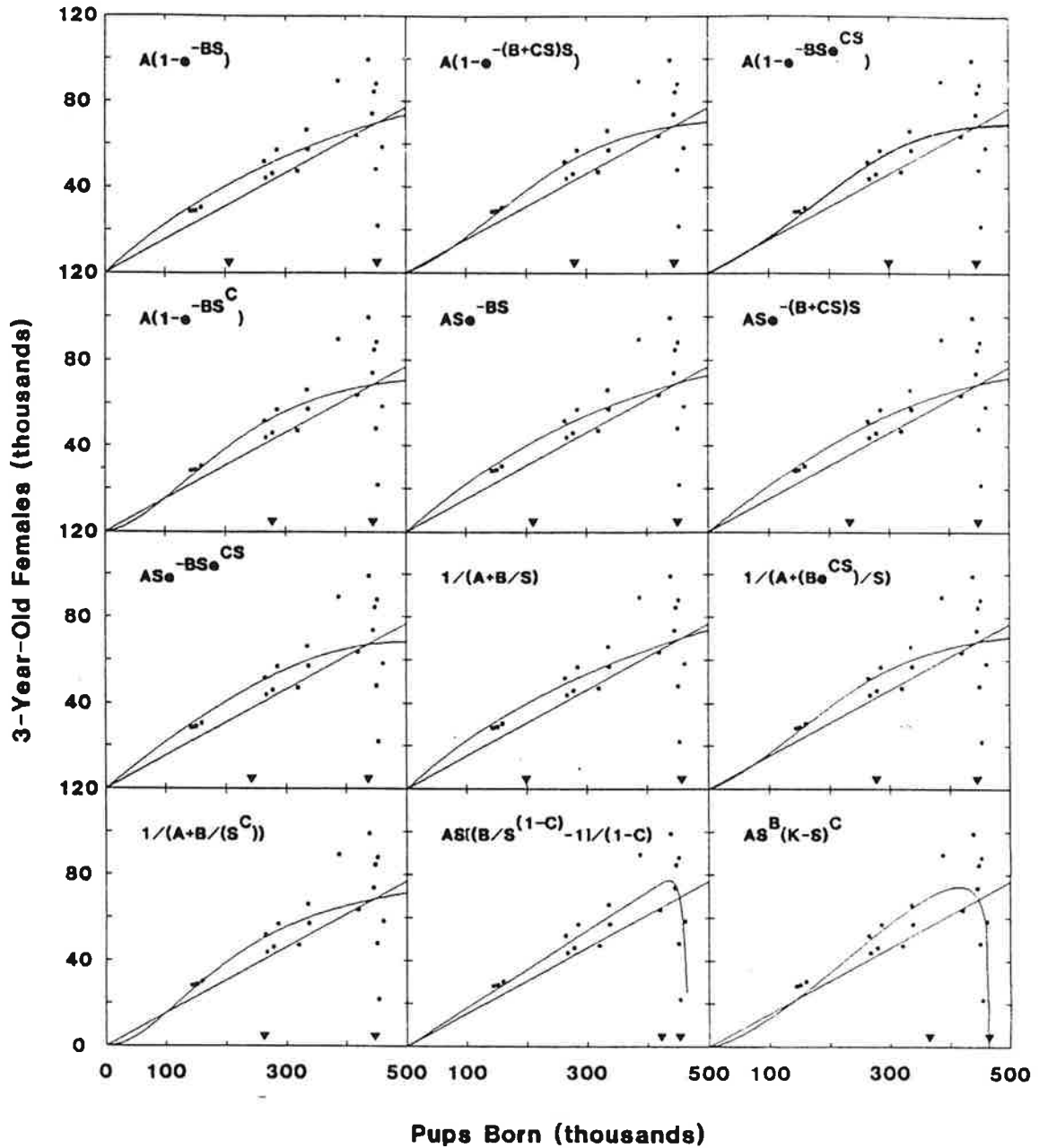


Fig. 4. Stock-recruitment models from Table 1 used to fit estimated recruitment of 3-year-old females (Y-axes) to number of pups born (X-axes). Data are adapted from Chapman (1973) and are for the years 1920-22 and 1950-65. Except for the generalized logistic (Richards 1959 and Allen 1976) models (middle and right of bottom row, respectively) the fitted models are visually similar. However, these models result in substantially different estimates of MNPL (left triangles just above X-axes). Estimates of K (right triangles) are much less variable.

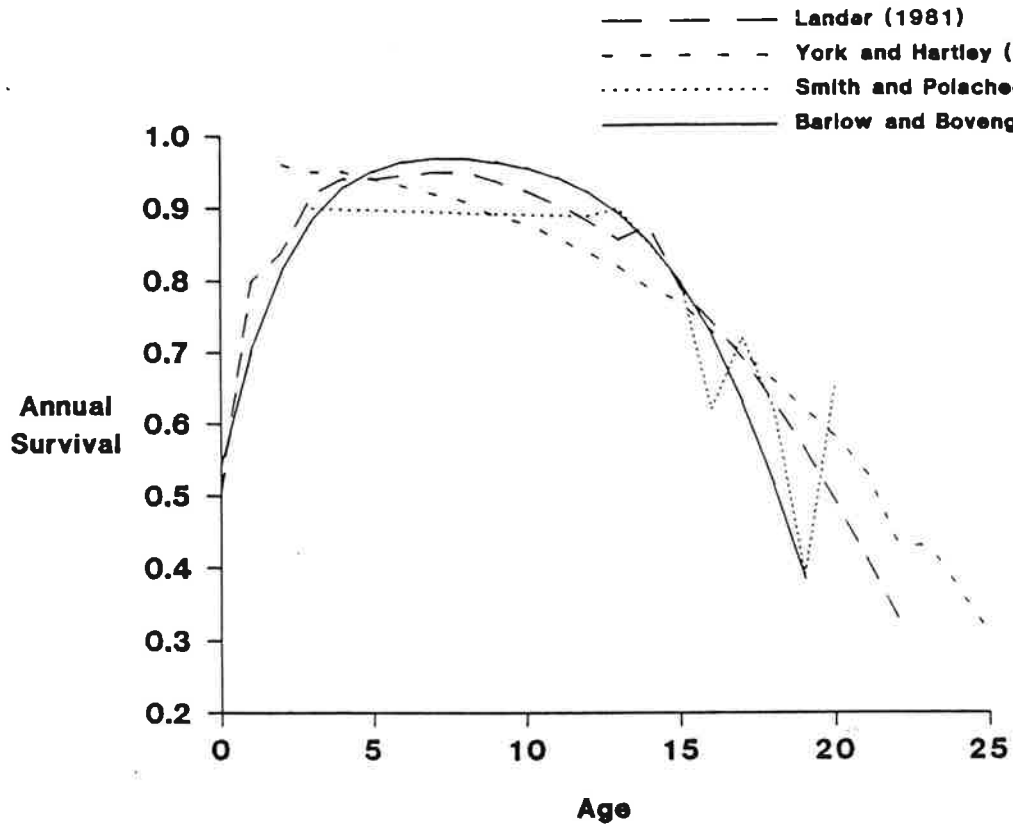


Fig. 5. Variability in age-specific equilibrium survival rates for female northern fur seals from the life tables of Lander (1981), York and Hartley (1981), Smith and Polacheck (1981), and Barlow and Boveng (1991).

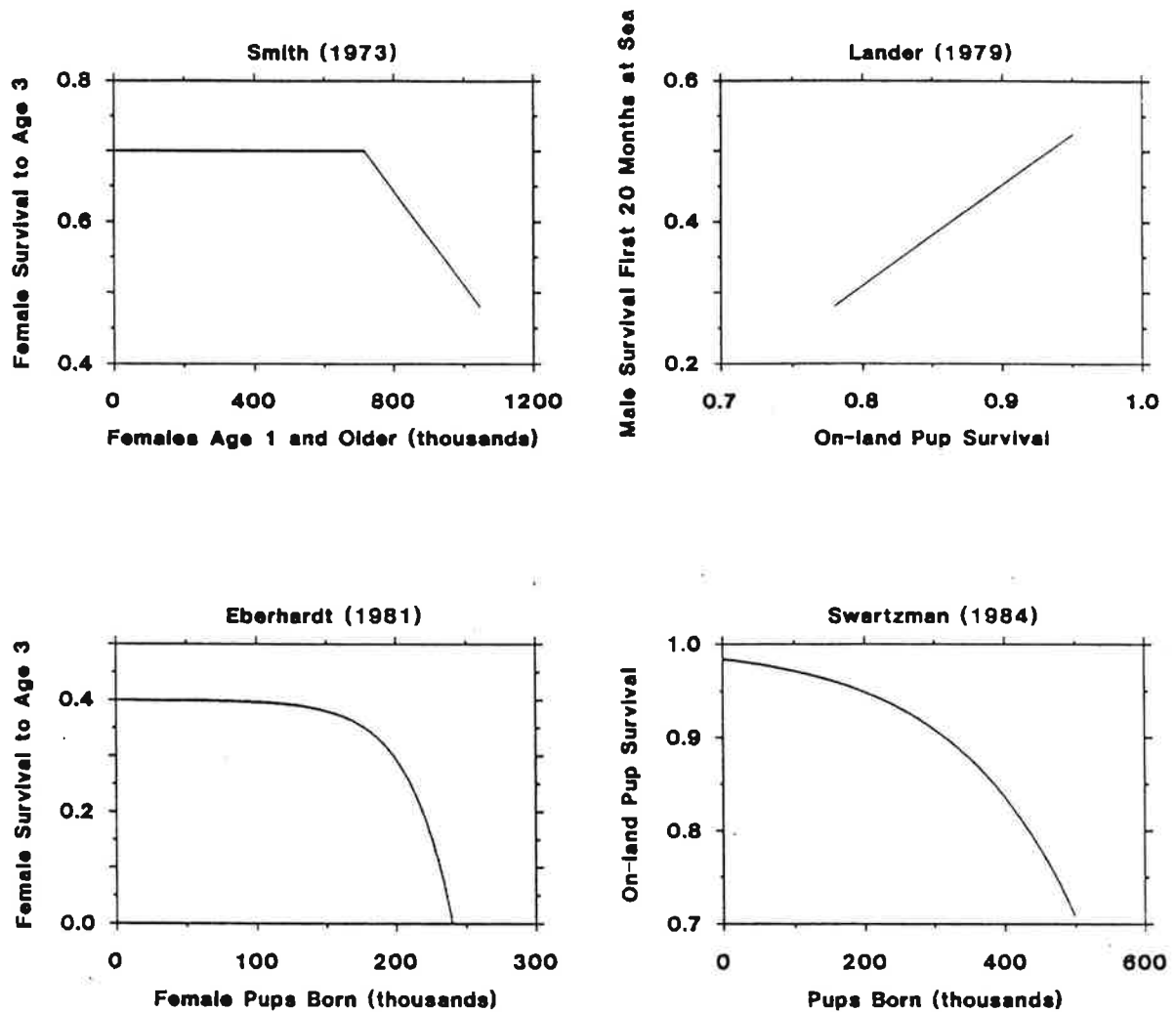


Fig. 6. Density-dependent mechanisms used in numerical modeling of northern fur seal population dynamics, including female survival from birth to age 3 (Smith 1973 and Eberhardt 1981), on-land pup survival (Swartzman 1984), and survival for the first 20 months at sea as a function of on-land survival (Lander 1979).

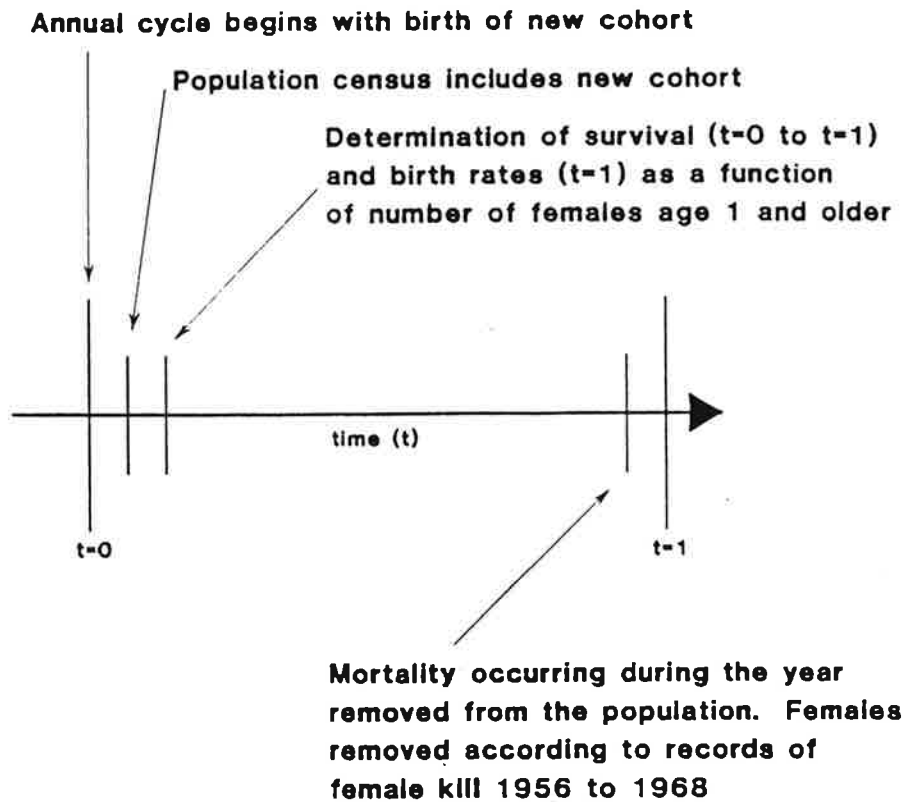


Fig. 7. The annual cycle of northern fur seals as modeled in these repetitive simulations.

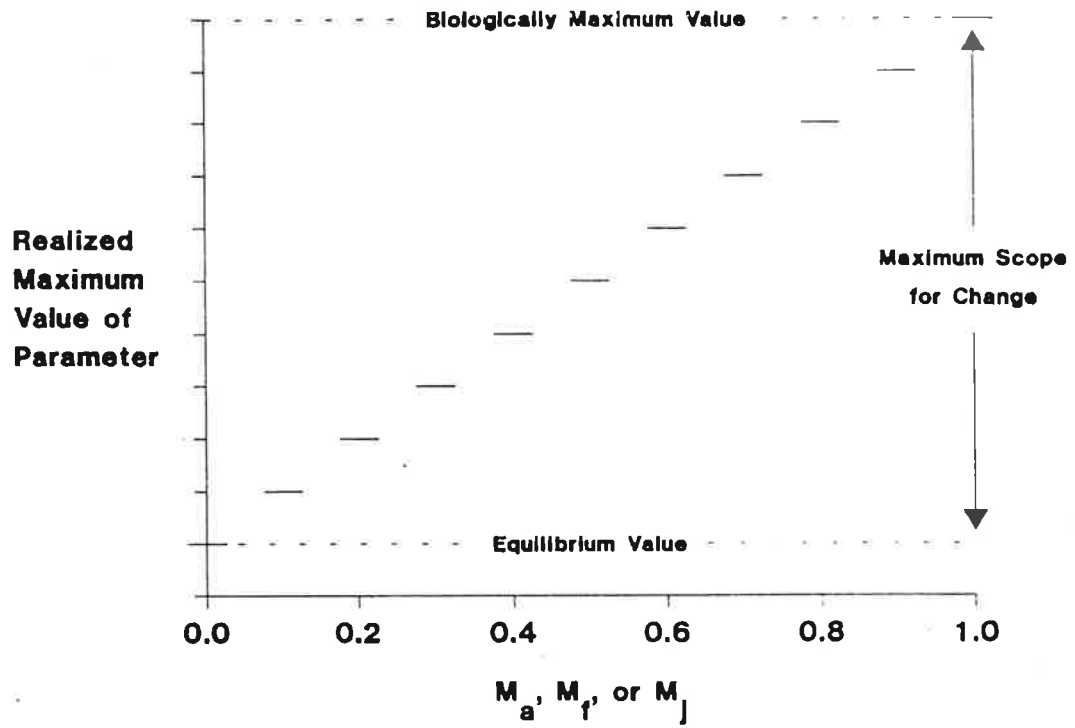


Fig. 8. Realized maximum values and scope for density-dependent change of life table parameters as determined by the input parameters M_a , M_f , and M_j (from Smith and Polacheck 1984). See Table 2 for biologically possible maximum values and equilibrium values.

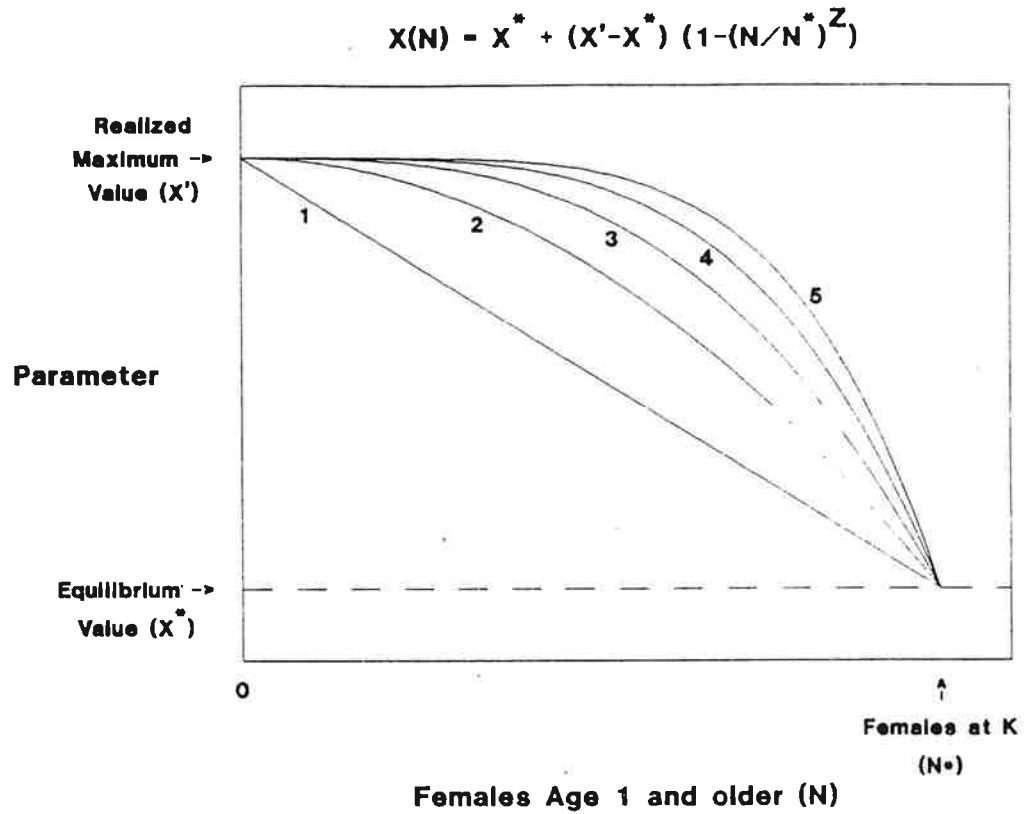


Fig. 9. Density dependence of vital parameters determined by the general Allen (1976) function and used by Smith and Polacheck (1984). Each line is labeled with the Z value used to generate that line.

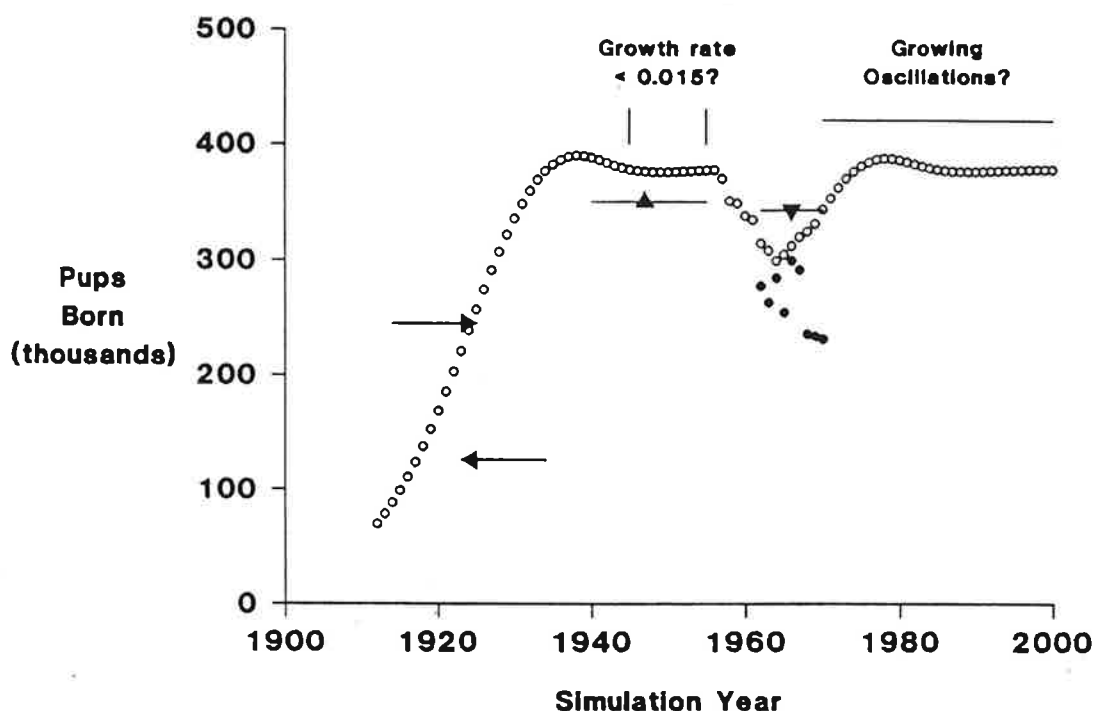


Fig. 10. The five validation criteria used to accept or reject simulations. The first criterion was the growth rate in the interval 1912-24. If the growth rate was within acceptable limits, the pups numbers passed between the two arrows on the left. The second criterion was the lower limit (350,000) for the maximum annual pup number in the interval 1940-55. The third criterion was the annual growth rate in the interval 1945-55, which had to decrease to less than 0.015 for at least 1 year. The fourth criterion was the number of pups born annually in the interval 1962-70, which must have dropped to less than 342,700 for at least 1 year. The final criterion rejected the simulation on the basis of abnormal behavior, particularly growing oscillations after 1970. Hollow circles are the pup numbers from a simulation. Also shown (filled circles) are the pup estimates for the interval 1962-70 from Briggs and Fowler (1984).

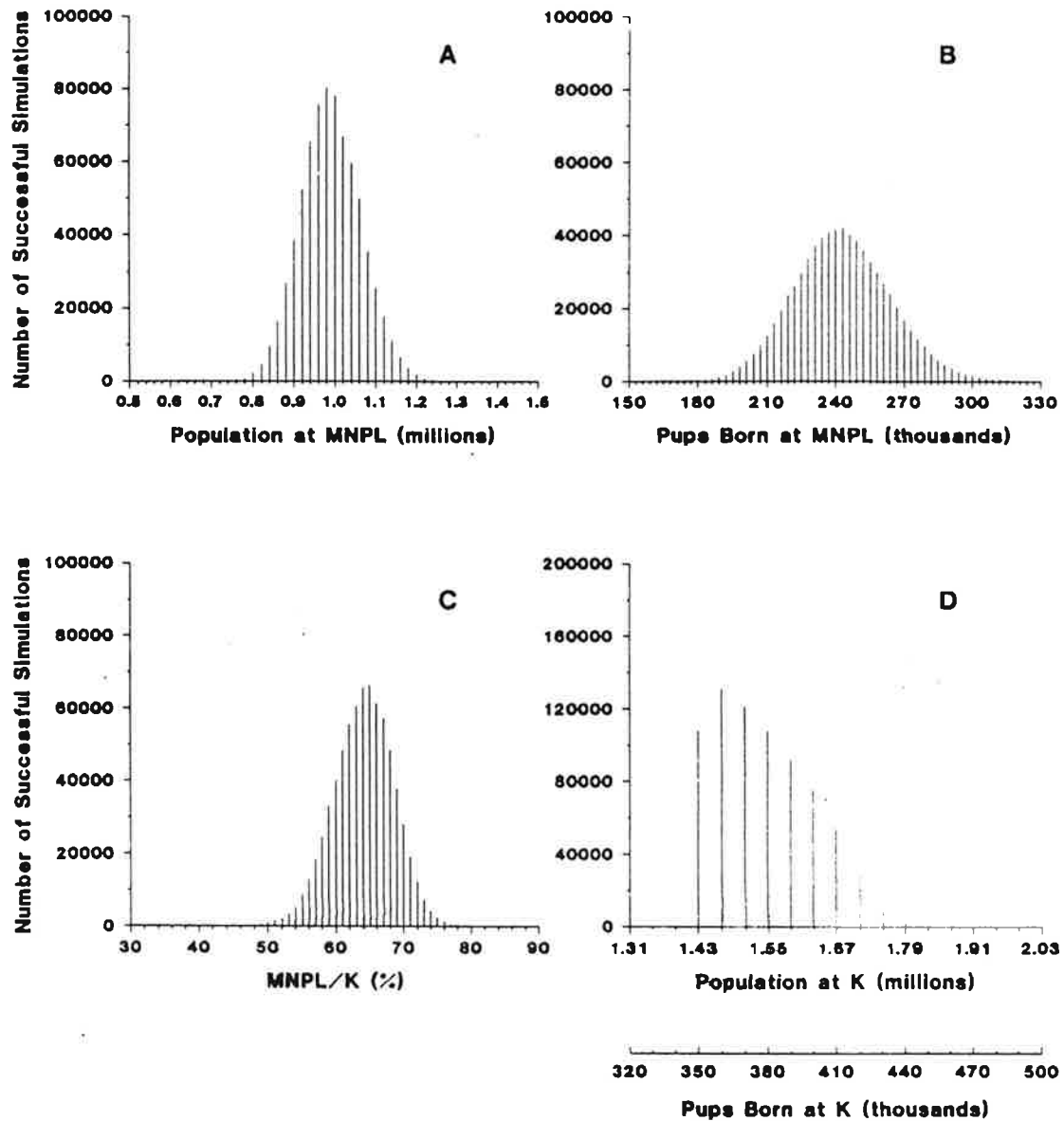


Fig. 11. Frequency distributions for five population measures from simulations satisfying original validation criteria ($n = 736,629$). Population measures include A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K.

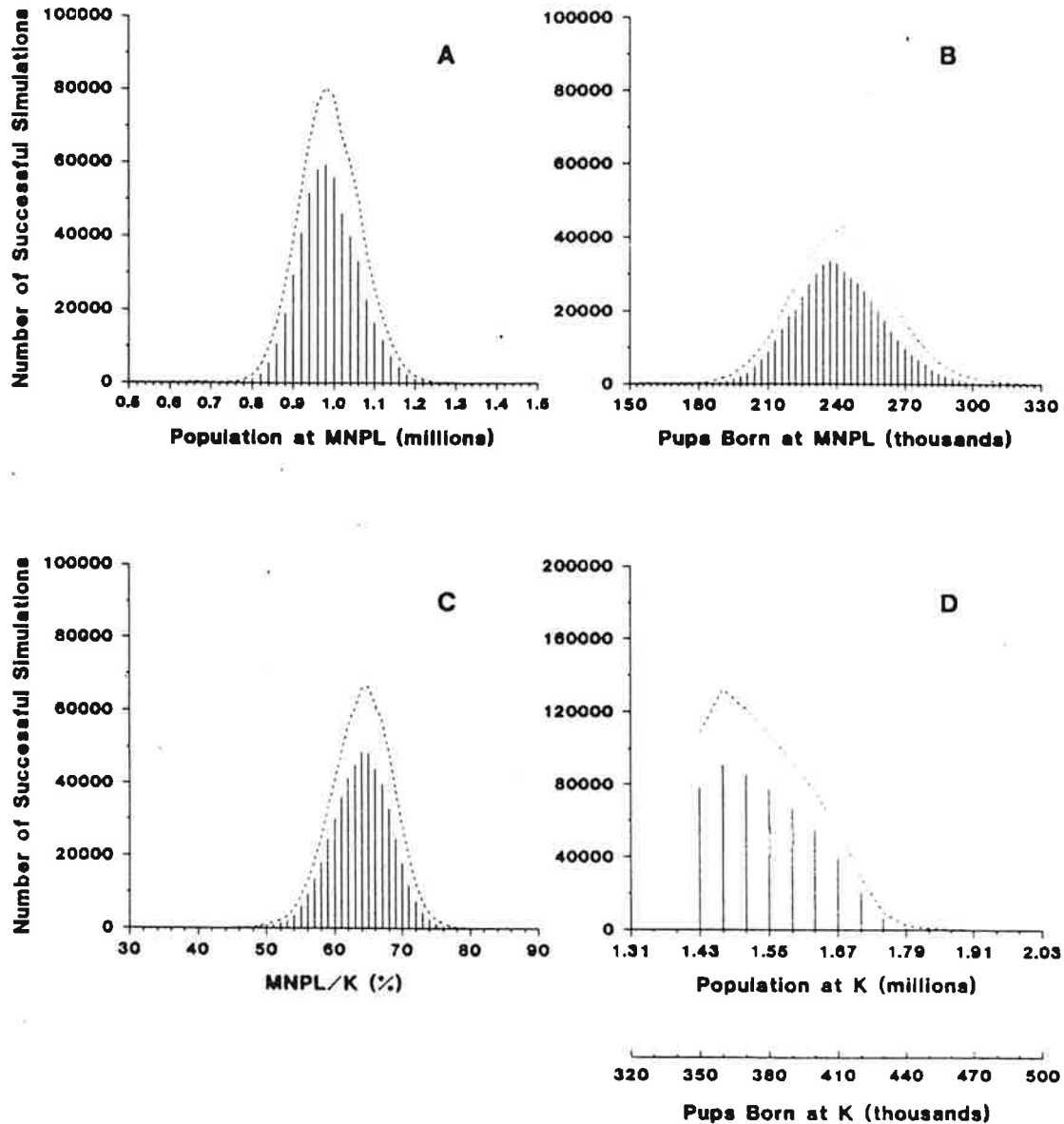


Fig. 12. Frequency distributions for five population measures ($n = 524,362$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Growth rates limits for interval 1912-24 narrowed to 0.06 and 0.10. The dotted line corresponds to results from Figure 11, with the original validation criteria (where growth rate limits were 0.05 to 0.11).

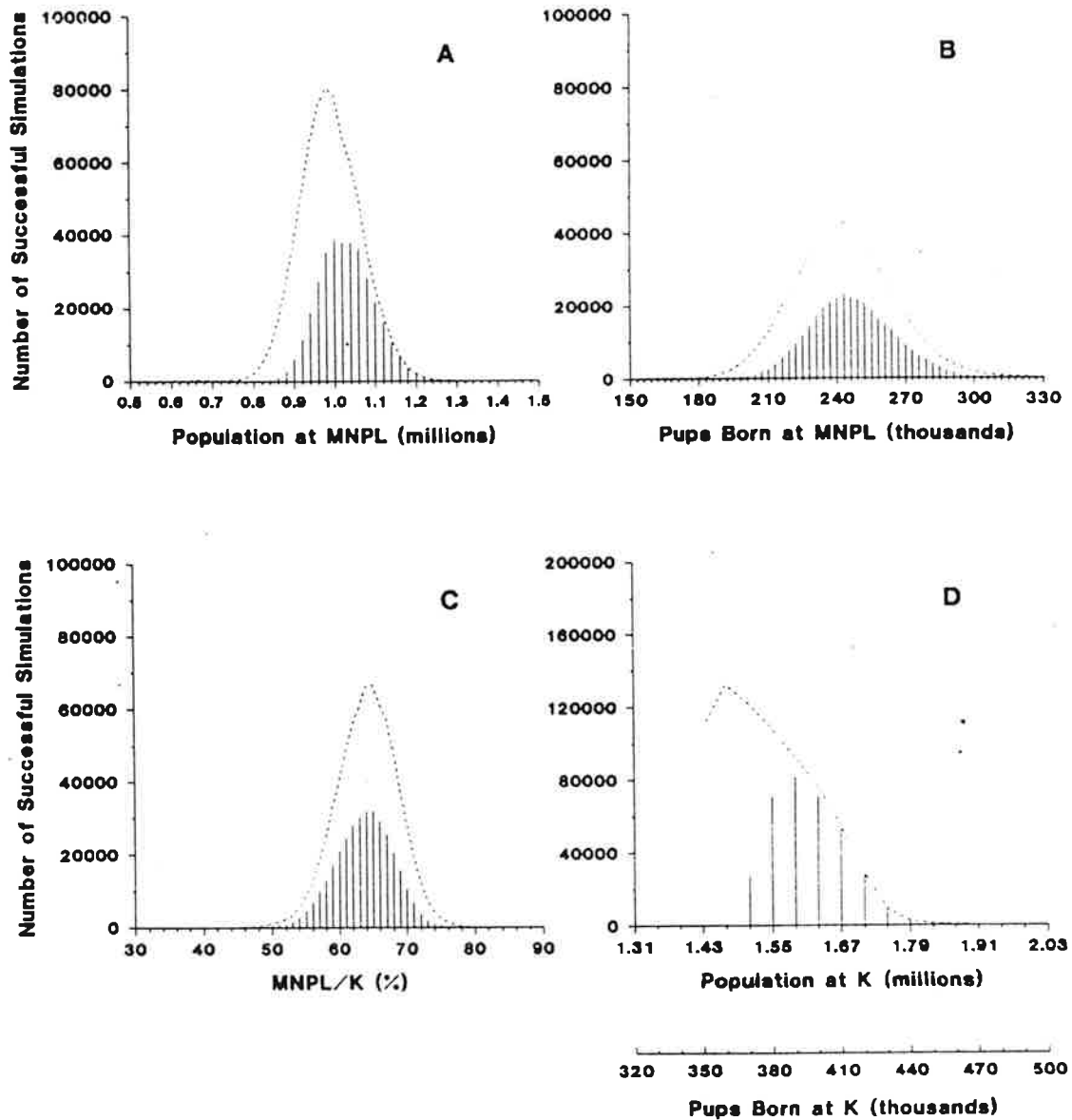


Fig. 13. Frequency distributions for five population measures ($n = 347,208$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Lower limit for maximum annual number of pups born in the interval 1940-55 increased from the initial level of 350,000 to 381,000. The dotted line corresponds to results from Figure 11, with the original validation criteria.

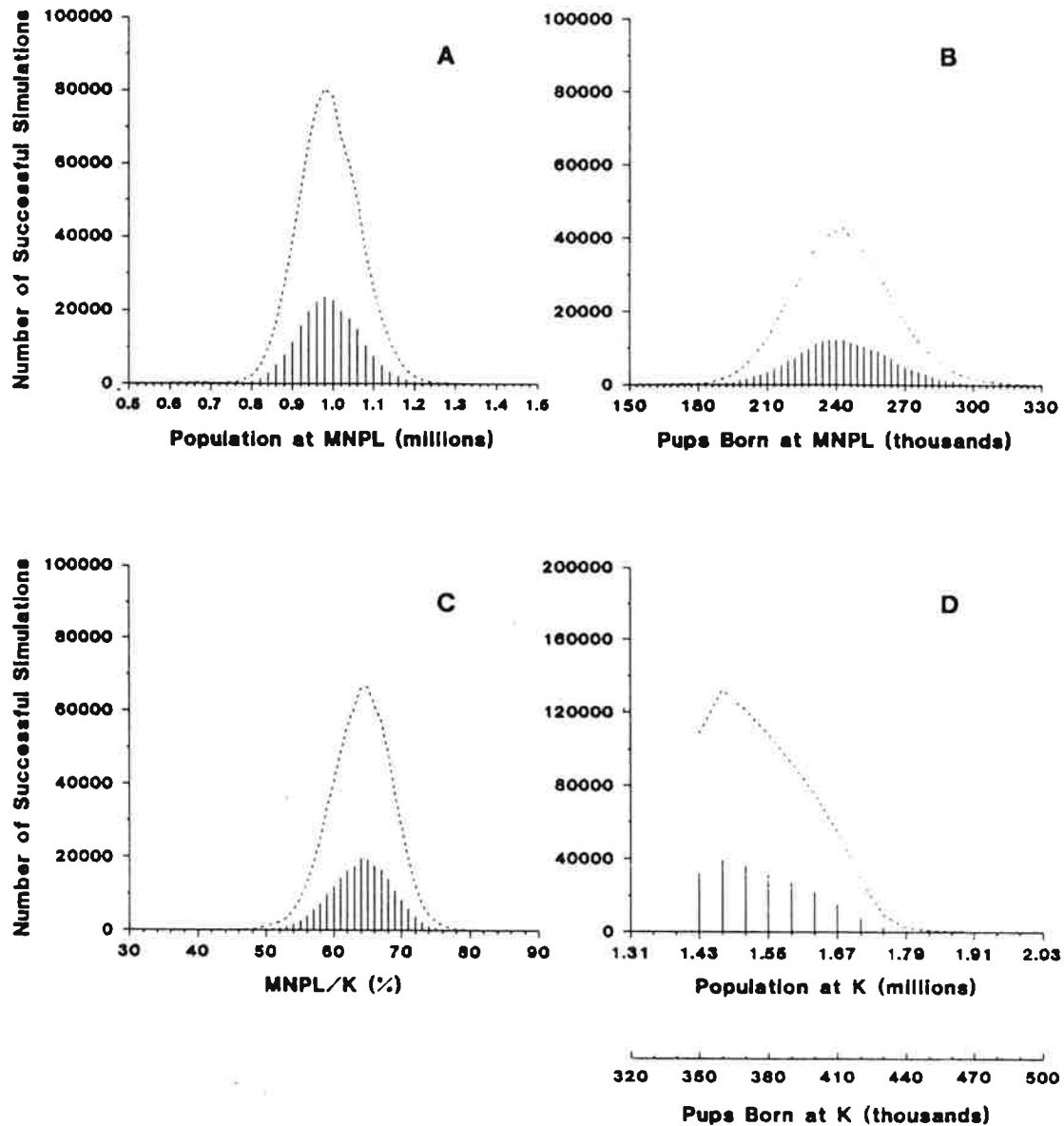


Fig. 14. Frequency distributions for five population measures ($n = 220,034$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. M_a and M_f parameters limited to six values (0.0, 0.2, 0.4...1.0) rather than eleven (0.0, 0.1, 0.2...1.0). The dotted line corresponds to results from Figure 11.

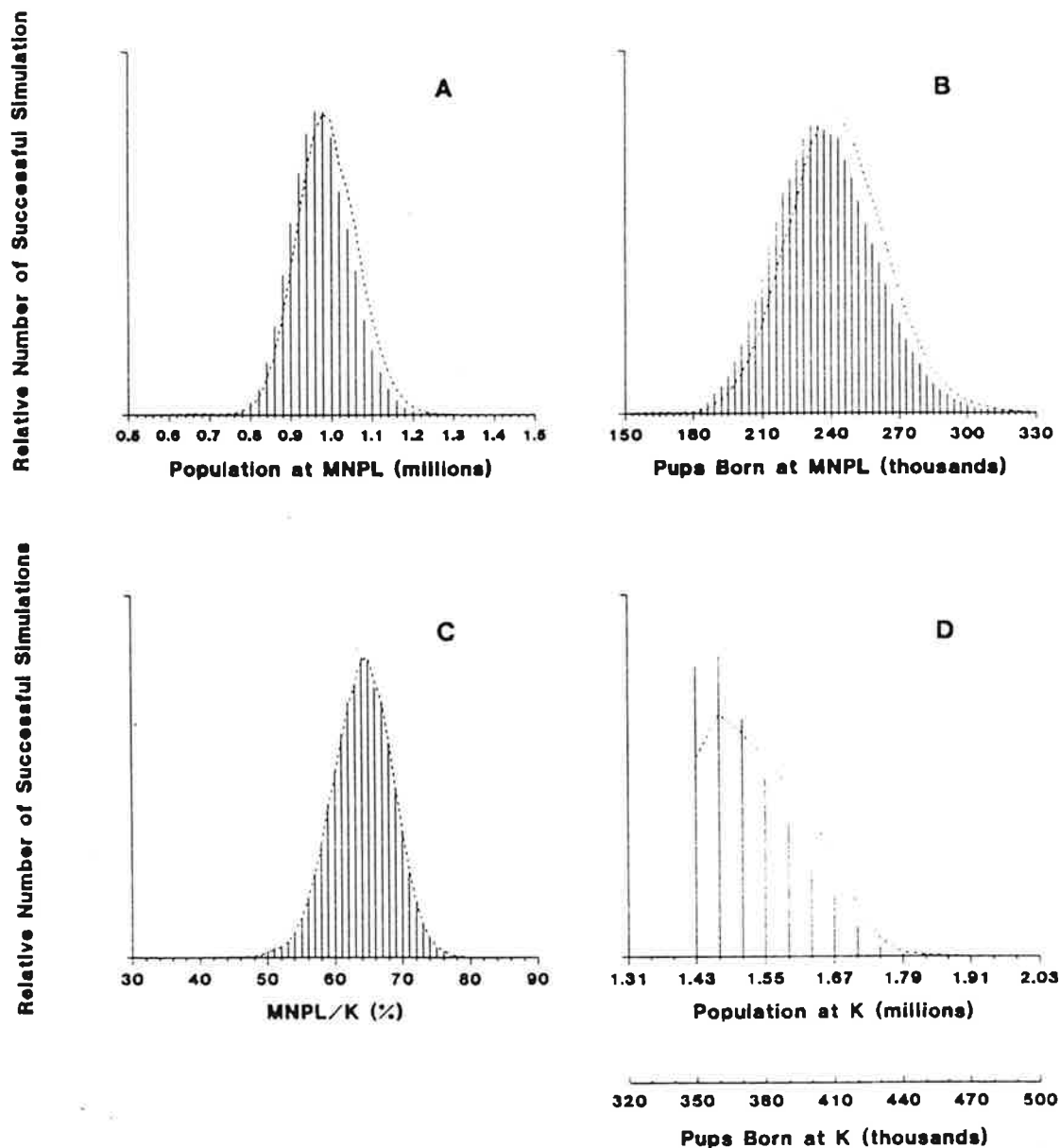


Fig. 15. Relative frequency distributions for five population measures ($n = 736,629$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Distributions are weighted by the error between observed annual pup production and pups born in the model during the interval 1962-70. The dotted line corresponds to results from Figure 11. To facilitate comparison, all distributions are scaled to sum 1.0.

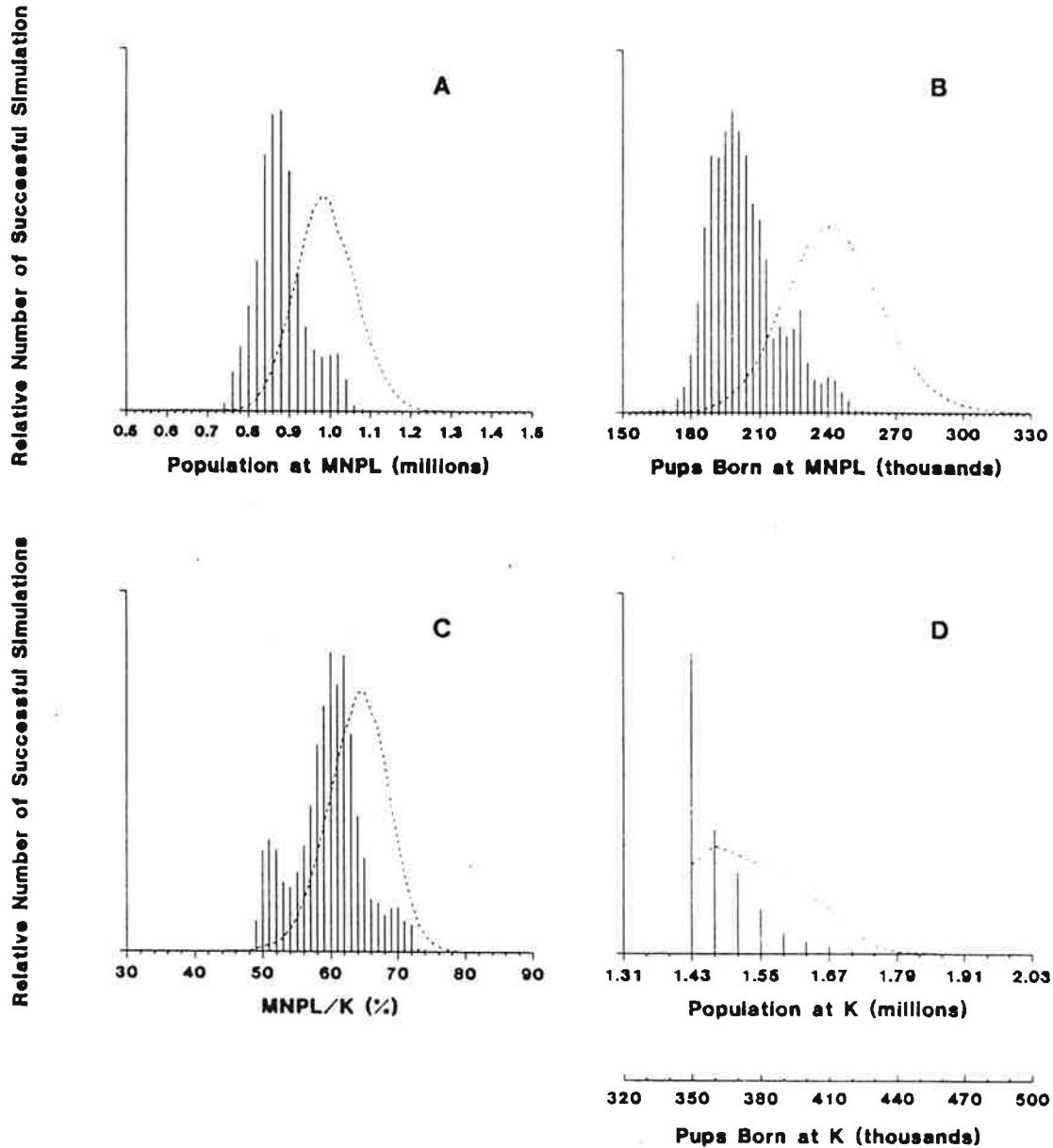


Fig. 16. Relative frequency distributions for five population measures ($n = 6279$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Distributions are weighted by the error between observed annual pup production and pups born in the model during the interval 1962-70. Only simulations with error in the lower 10% of the error range are included. The dotted line corresponds to results from Figure 11, with the original validation criteria. To facilitate comparison, all distributions are scaled to sum 1.0.

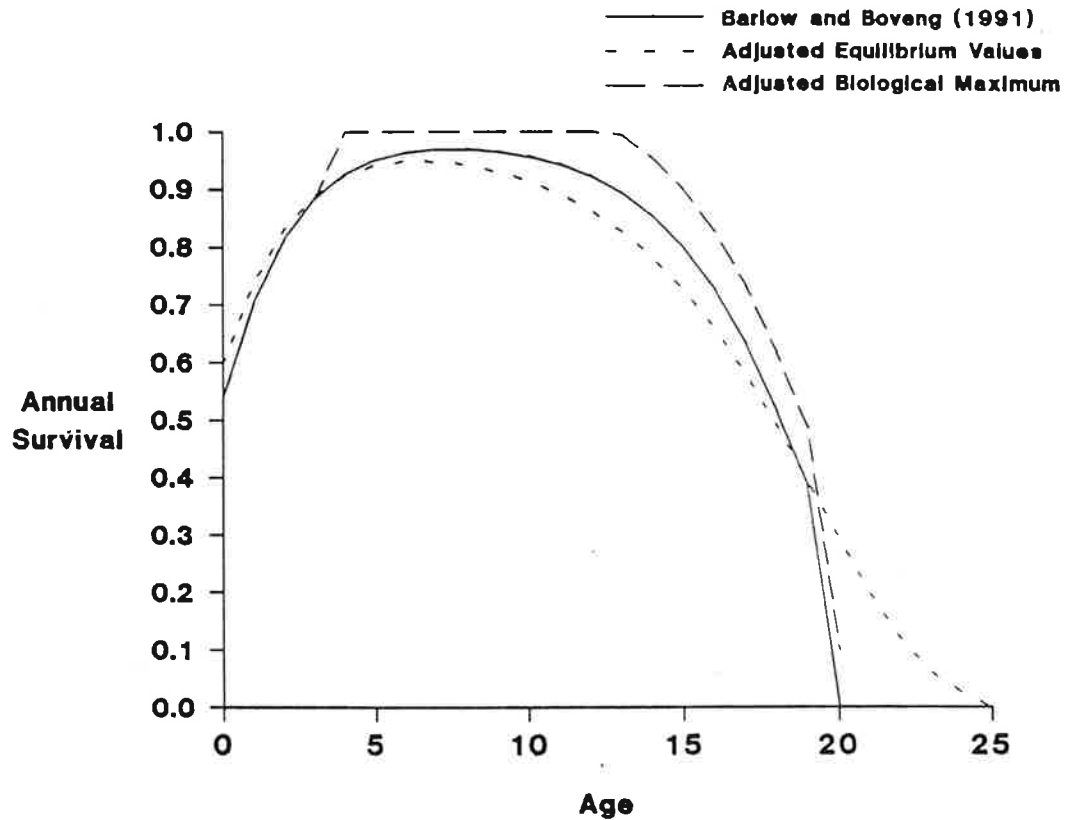


Fig. 17. Comparison of age-specific survival values for northern fur seal females as used in the repetitive simulations, including equilibrium values from Barlow and Boveng (1991), adjusted equilibrium values with slightly greater juvenile survival and lower adult survival (modified arbitrarily but constrained to result in equilibrium growth), and an adjusted schedule of biologically possible maximum values (biologically possible values limited to no more than 10% of corresponding equilibrium values). The latter two survival schedules were used to test the sensitivity of the repetitive simulation approach to a different life table and to limited scope for density-dependent change, respectively.

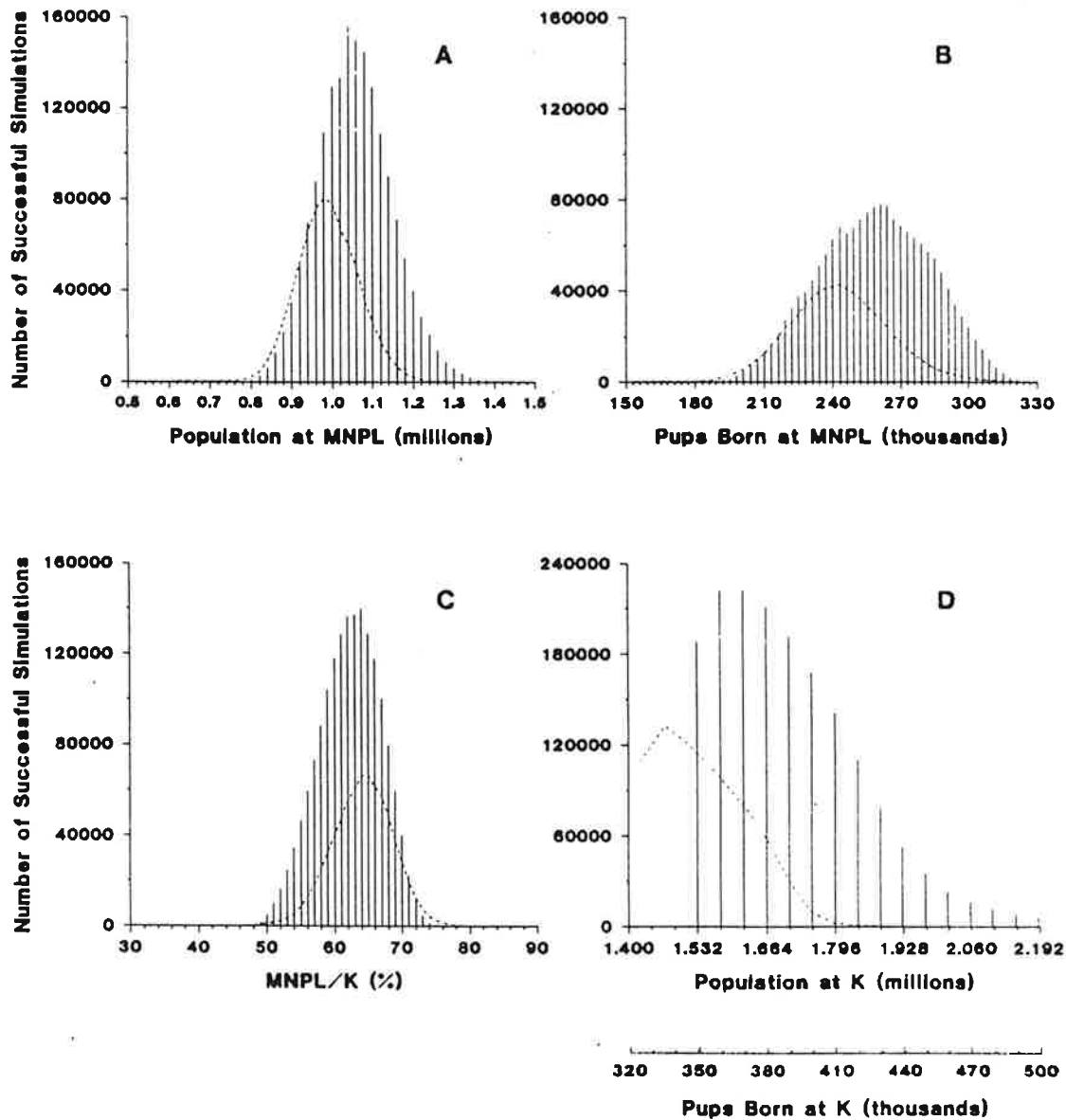


Fig. 18. Frequency distributions for five population measures ($n = 1,697,491$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Results generated using an adjusted equilibrium survival schedule for females (see Fig. 17). The dotted line corresponds to results from Figure 11, with the equilibrium survival schedule from Barlow and Boveng (1991).

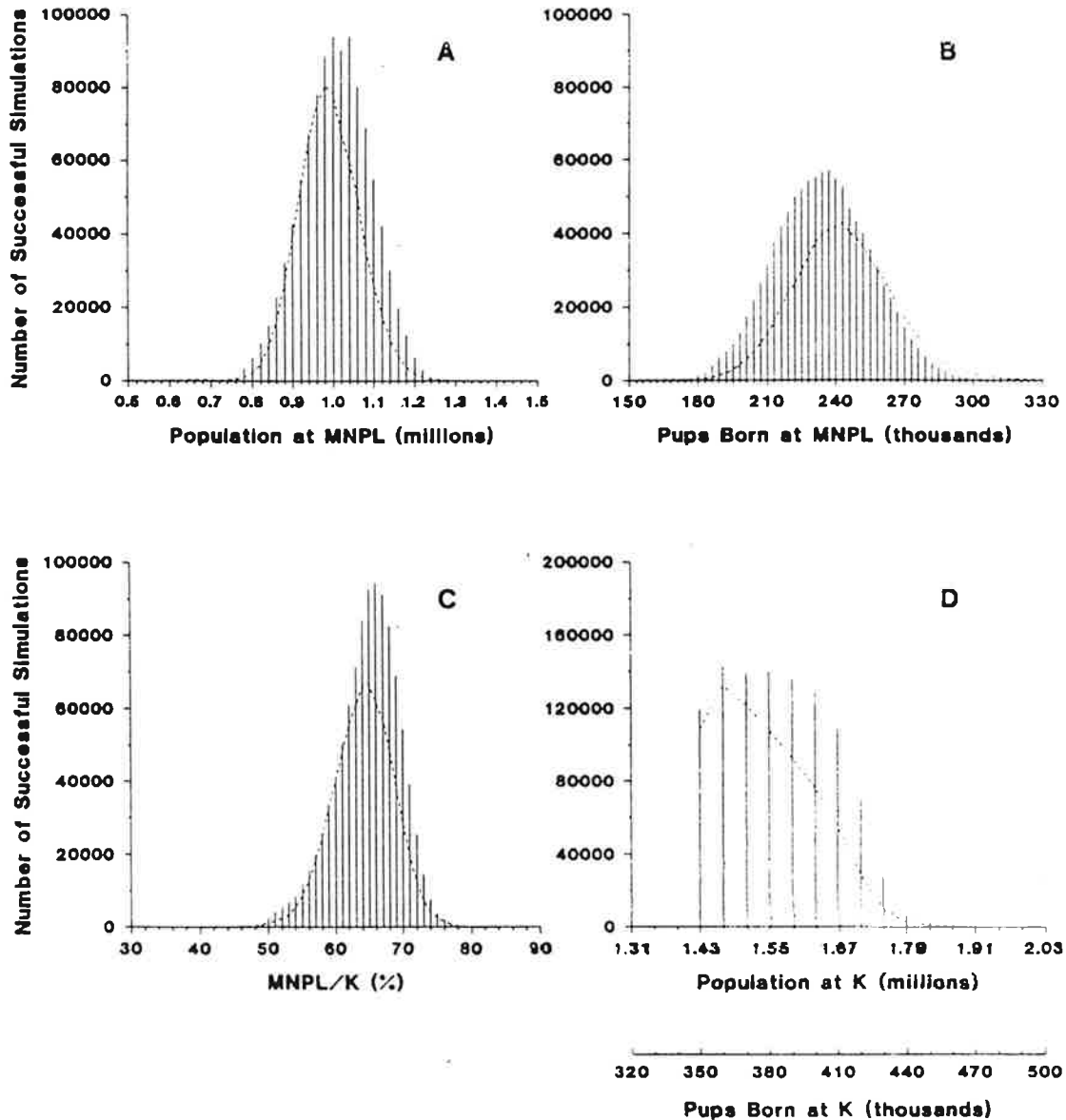


Fig. 19. Frequency distributions for five population measures ($n = 1,026,284$), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Results generated by limiting the scope for density-dependent change in adult survival to no greater than 10% of the equilibrium value (see Fig. 17). The dotted line corresponds to results from Figure 11, where a biologically possible maximum value of 1.0 was used for all adult female survival rates.

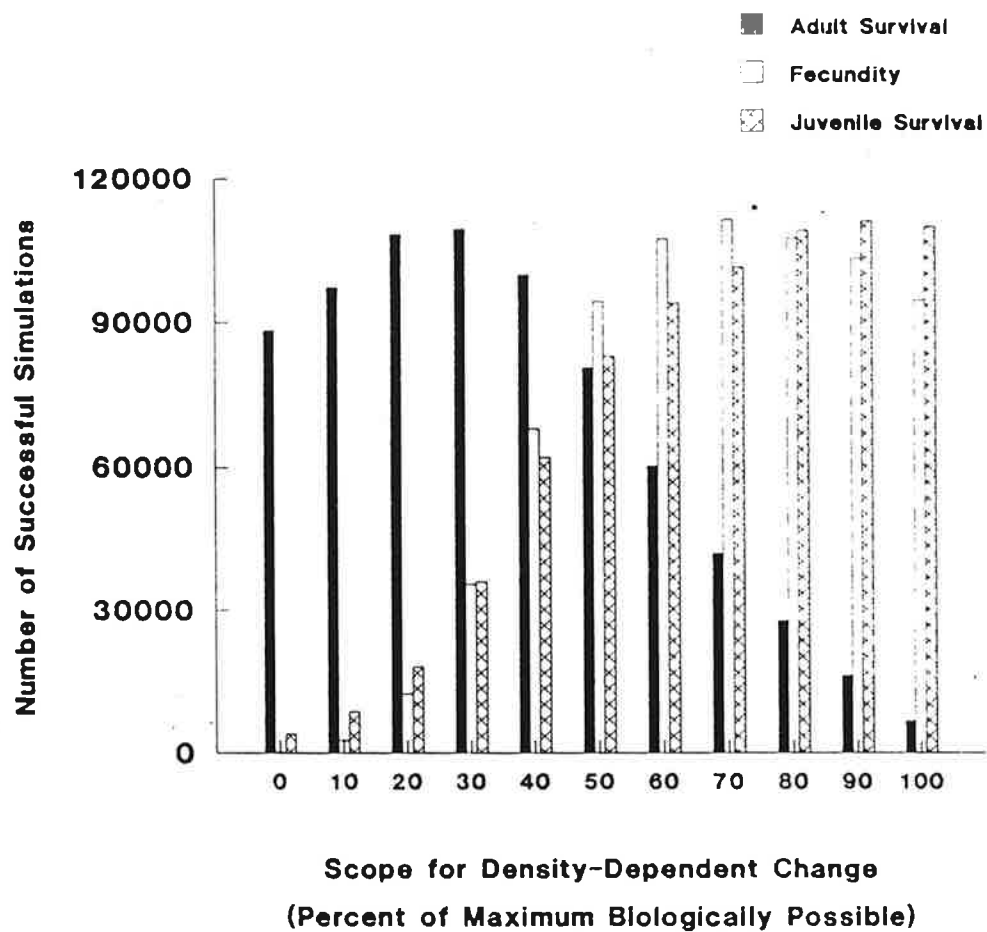


Fig. 20. Frequency distributions for values of M_a , M_f , and M_j recorded from successful simulations ($n = 736,629$).

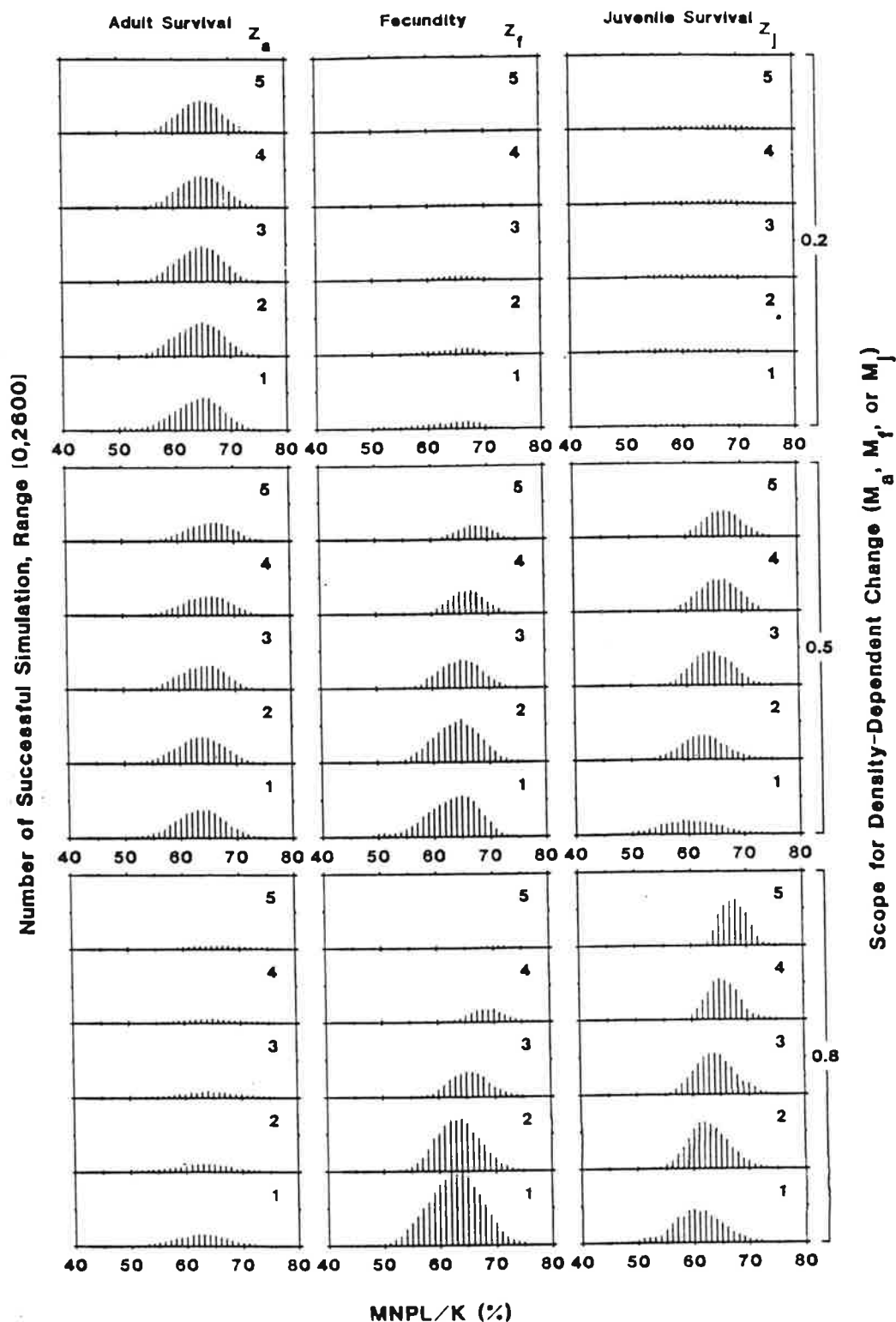


Fig. 21. Frequency distributions of $MNPL/K$ as determined by degree of nonlinearity (Z_a , Z_f , or Z_j) and scope for density-dependent change (M_a , M_f , or M_j) in the functions regulating adult female survival, fecundity, and juvenile survival, respectively.